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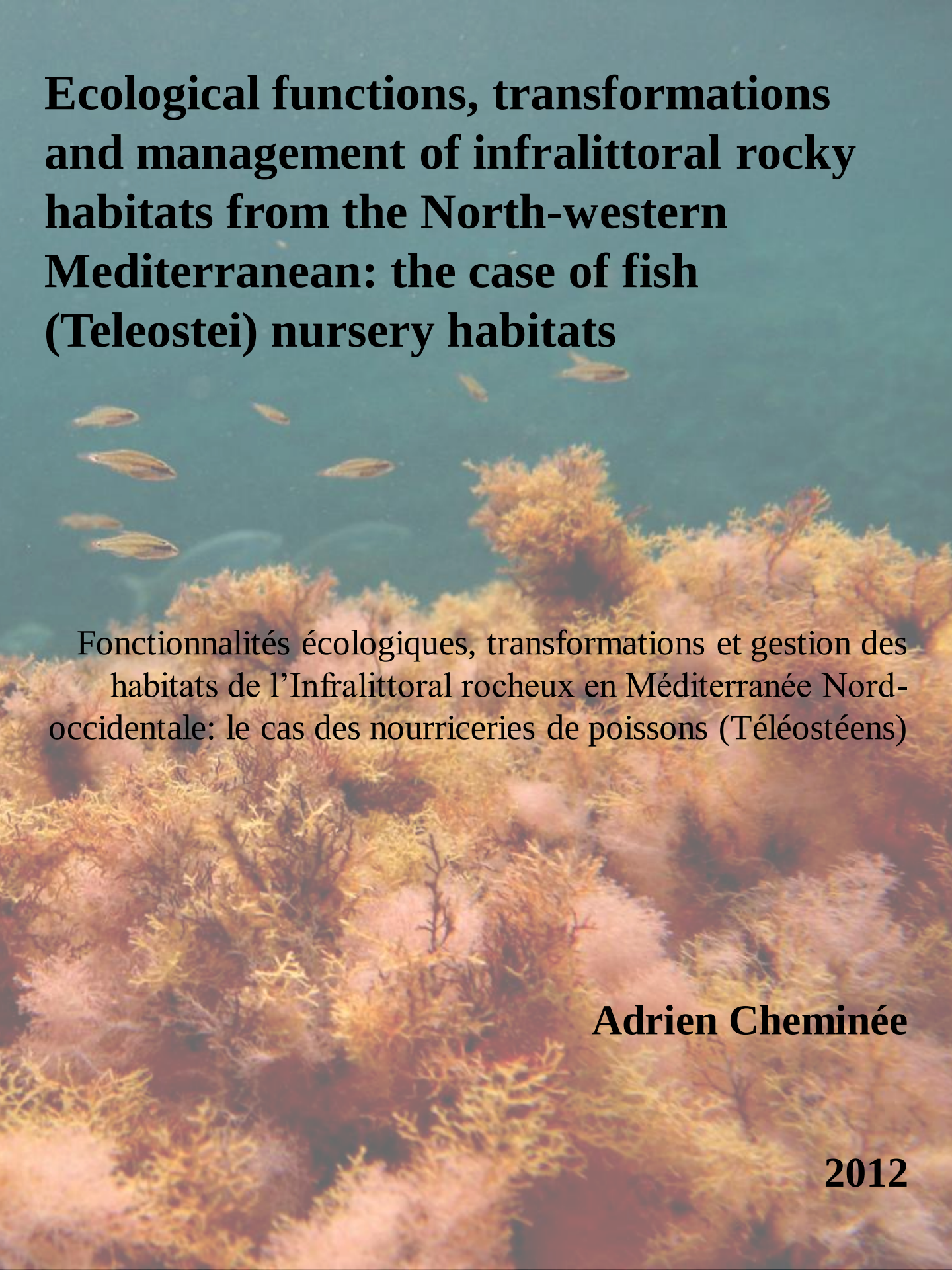

Fonctionnalités écologiques, transformations et gestion des habitats de l'Infralittoral rocheux en Méditerranée Nord-occidentale: le cas des nourriceries de poissons (Téléostéens)

Adrien Cheminée

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T H E S E

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Adrien CHEMINEE

Ecological functions, transformations and management of infralittoral rocky habitats from the North-western Mediterranean: the case of fish (Teleostei) nursery habitats

Fonctionnalités écologiques, transformations et gestion des habitats de l'Infralittoral rocheux en Méditerranée Nord-occidentale: le cas des nourriceries de poissons (Téléostéens)

Thèse dirigée par Patrice FRANCOUR

soutenue le 30 novembre 2012

Devant le jury composé de :

Mme. Laure FOURNIER – Membre invité
M. Patrice FRANCOUR – Directeur de thèse
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M. Frithjof KÜPPER – Rapporteur
M. Enrique MACPHERSON – Examinateur
M. Nicholas POLUNIN – Examinateur

« Ce qui sans doute importe plus que tout, c'est qu'ensemble nous parvenions à donner sens à nos contributions personnelles »

Francis Jeanson – *Citoyennetés, 2008*

« (…) à l'occasion du soixantième anniversaire du Programme du Conseil national de la Résistance, nous disions le 8 mars 2004, nous vétérans des mouvements de Résistance et des forces combattantes de la France libre (1940-1945), que (…) cette menace [la barbarie fasciste, ndla] n'a pas totalement disparu. Aussi, appelons-nous toujours à « une véritable insurrection pacifique contre les moyens de communication de masse qui ne proposent comme horizon pour notre jeunesse que la consommation de masse, le mépris des plus faibles et de la culture, l'amnésie généralisée et la compétition à outrance de tous contre tous. ». A ceux et celles qui feront le XXI^{e} siècle, nous disons avec notre affection : « Créer, c'est résister. Résister, c'est créer. » »

Stéphane Hessel – *Indignez-vous !, 2010*

Soupe de poissons de roche (Girelles, Rascasses, Labres, Serrans, Blennies, Gerles, …)

« La soupe de poissons, c'est comme la soupe de légumes, vous mélangez tout, vous faites cuire et vous passez ! L'idéal, c'est de varier les espèces le plus possible : la dominante est le poisson de roche auquel on ajoute tête de baudroie, tête et queue de congre ou de murène. Cela apporte du gélifiant qui lie la soupe et qui épaissit le bouillon. Ça a son importance. Il est très bon d'ajouter des crustacés : une poignée de crevettes ou de crabes ou de bernard l'hermite (avec les anémones dessus). Plus on met des choses différentes, plus on apporte de goûts. Il faut savoir faire avec ce qu'on a, parfois on fait une soupe avec pas grand-chose, parfois on fait une soupe riche. C'est pas la peine de vider les poissons sauf les grosses rascasses qui viennent de manger et qui ont une boule au niveau du ventre.

Vous faites revenir un kilo de poissons avec un gros oignon dans de l'huile d'olive. Si on en met trop, ça donne un goût sucré. Vous salez aussi car ça fait ressortir les sucs. Vous faites revenir tant que vous pouvez, en touillant, jusqu'à ce que ça accroche un peu au fond de la gamelle, que ça soit quasiment une bouillie. Au début, ça ne sent pas très bon, après, les saveurs se dégagent. Si vous voulez 2 ou 3 tomates, vous pouvez en mettre. Il n'y a pas de recette absolue, c'est comme la soupe aux légumes, on la fait jamais pareil sinon c'est triste ! Il faut seulement se méfier l'été car avec la chaleur la tomate fait virer la soupe. Vous ajoutez 2 litres d'eau, piment, fenouil, thym-laurier, un quart de tête d'ail (si on le met trop tôt, il perd de son arôme).

Les proportions c'est en fonction de son goût… – J'en connais qui font des infusions de thym, c'est bon mais il n'y a pas besoin de mettre du poisson dedans, plutôt du miel. – ça frémit et ça mijote pendant une petite heure. Ensuite, au moulin ! L'idéal est de mixer le tout, faire un gros brassage, puis tout verser dans un chinois et mixer la soupe dans le chinois. Souvent, je dis au client : « Ne vous embêtez pas à faire un kilo de soupe de poissons. Passez-y une matinée s'il faut mais faites-vous une bonne quantité que vous congelez ensuite ». En soi, c'est pas beaucoup de travail mais ce qui est un peu long, c'est de la passer. Après, vous ajoutez une pointe de couteau de safran et si nécessaire sel, piment. Vous réchauffez un coup avant de servir avec, selon les goûts, des croutons aillés et du fromage râpé. Souvent la rouille change le goût de la soupe. La rouille, c'est pour rattraper une mauvaise soupe !

Une variante consiste à mettre quelques nouilles à cuire dans la soupe juste après l'avoir passée, à rajouter safran et assaisonnement, et à la servir avec du fromage râpé.»

Pépito, pêcheur de Giens – ***in : Saveurs marines, brochures du CLPMEMV***

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Remerciements / Acknowledgments / Agradecimientos

Pour commencer, je souhaite remercier mon directeur de thèse, le Pr. Patrice Francour, grâce à qui cette thèse s'est déroulée dans de très bonnes conditions, ainsi que les membres du jury qui me font l'honneur d'y participer. Cette thèse s'est déroulée dans le cadre du projet de recherche FOREFISH, parrainé par la Fondation Total, dont je souhaite remercier Laure Fournier pour son soutien constant au cours de ce projet. Afin de rentrer plus dans les détails de ces remerciements, voici un petit historique de cette thèse… : je souhaite au fil de ce récit en profiter pour remercier toutes celles et ceux qui, au cours de ces dernières années, ont rendu ce projet possible et agréable à vivre. Je suivrai donc un ordre chronologique, afin de bien retracer cette histoire !

En quelques sortes, le début de l'aventure remonte à 10 ans en arrière : j'ai alors réalisé pour mon diplôme de Maîtrise un stage à la Mission Océans et Côtes du WWF, à Marseille, au printemps 2002. Il s'agissait de rédiger les fiches d'inscription d'une dizaine de sites mahorais au titre de la Convention sur les zones humides d'importance internationale (Convention de Ramsar). Je souhaite en remercier chaleureusement les membres de l'époque : ma maître de stage Catherine Gabrié, Denis Ody, Laurent Debas, Olivier Musard, Sébastien Mabile, Amandine Eynaudi, ainsi que mes professeurs de Maîtrise Nardo Vicente, Eric Vidal et Jean-Marie Triat, pour m'avoir fait découvrir et aimer l'étude et la protection des milieux naturels, notamment côtiers. Merci également Catherine de m'avoir encouragé à l'époque à partir en échange au Canada, à l'Université McGill : ce fut une expérience tellement positive ! Merci également aux membres du GRASM, association de plongée et organisme de formation pro, pour m'avoir dès cette époque formé à la plongée sous-marine : N1 avec Loic, Cyril, puis plus tard N3 et CAH avec Julien, Serge.

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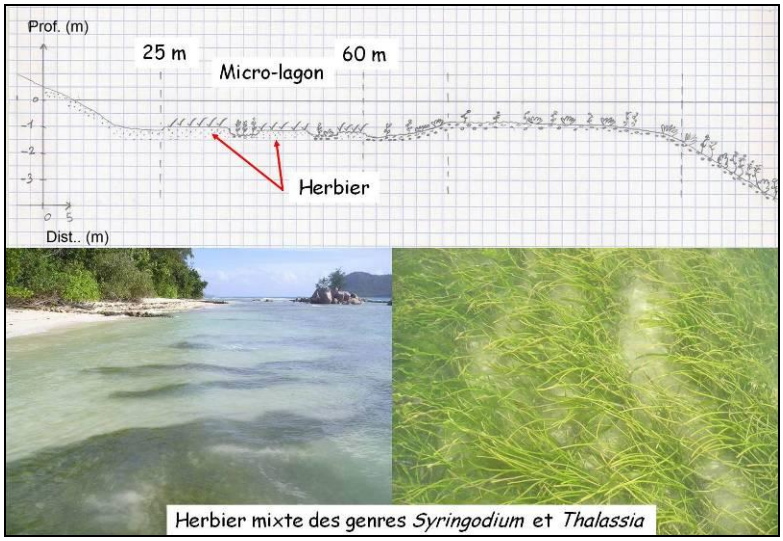
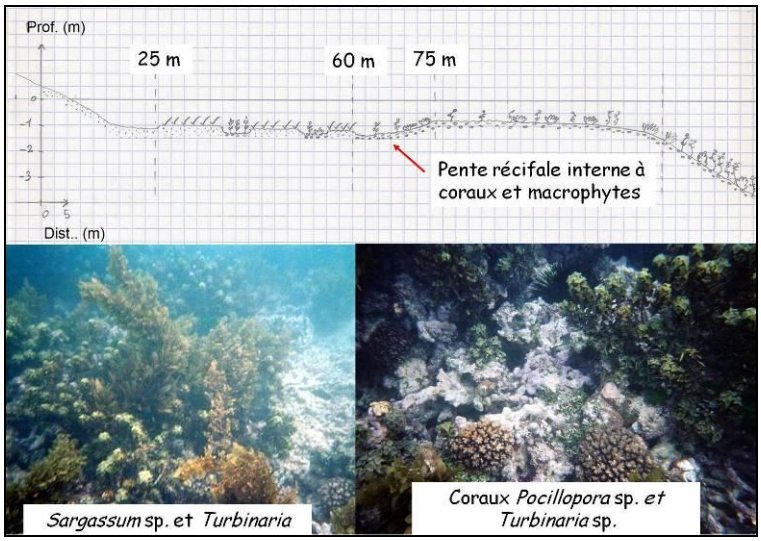
Chapter I. General introduction





Typical habitats of an infralittoral seascape of Praslin Island, Seychelles, Indian Ocean (28th of July 2007) - modified from Oberlinkels et al. (2007). Since early in the history of marine ecology (70s), in tropical seascapes, habitats such as mangroves, back-reef seagrass meadows or fringing coral reefs are known to be key-habitats both for their ecological role within the fish life cycle and for the ecosystem services they provide to humans. Their cartography is therefore a common tool used for coastal management planning. In the Mediterranean, knowledge on essential habitats and such management approaches are more recent.

Chapter I. General introduction

1.1 Context

The infralittoral environment (*sensu lato*) may be subdivided in different sub-units of homogenous abiotic and biotic characteristics, forming a mosaic-like structure. Depending on the considered spatial scale, units may be called ecosystem, habitat or micro-habitat (Chapman, 1995) and are characterized by their biotope and biocenosis. In this PhD thesis, I refer to this definition of "habitat", although it has been defined in many different ways (Hall et al., 1997). Since quite recently in the history of ecology, this mosaic is referred to as "seascape(s)" (Pittman et al., 2011), by analogy to the continental "landscapes". Seascape dimensions usually range from few meters to few kilometers. August (1983) established that the combination of biotic and abiotic characteristics determines seascape and individual habitat tri-dimensional structure by shaping their heterogeneity (composition and ordination of sub-units) and their complexity (tri-dimensional architectural arrangement of each sub-unit).

In a given coastal area, numerous stakeholders challenge the seascape: human activities generate pressures on the natural environment that tend to cumulate at the interface between land and sea, along the coastline. These pressures may reach threshold levels and generate impacts and threats on each unit of the seascape to various degrees. Due to the multiplication of stakeholder conflicts and to threats on marine resources of the Infralittoral (Coll et al., 2010; Mouillot et al., 2011), coastal managers need to identify priority stakes and to define management objectives and action plans for coastal areas. Defining such priorities requires first an analysis of both land- and sea-scapes in order to identify units where the interaction between natural components and anthropic pressures generate particularly worrying impacts. In this context, more particular attention is given to seascape units having a highly valuable role (i.e. ecological, social, or economical functions). From an ecological point of view, particularly important habitats are those playing a key role within marine organisms life cycle. In the case of fishes (Teleostei), for example, these roles will be notably adult spawning grounds (Koenig et al., 2000) and juvenile nursery habitats (Beck et al., 2001; Harmelin-Vivien et al., 1995).

In many cases, benthic and necto-benthic fishes experiment a bi-partite life cycle, with a pelagic dispersive larval phase and a more sedentary juvenile and adult benthic phase. Settlement is defined as the transition from pelagic larval habitats to benthic juvenile habitats. Recruitment is defined as the incorporation of older juveniles (recruits) into adult populations after their survival and growth within juvenile habitats. "Juveniles" include individuals from the smallest "settlers", just arrived from the pelagic habitat, to larger "recruits", i.e. settlers that survived, grew up in juvenile habitats, and are ready to join adult assemblages (Levin, 1994; MacPherson, 1998). In benthic habitats, a particular set of life history strategies display a separation (or at least some disjunction) between juvenile and

adults habitats (Beck et al., 2001). Furthermore, for given taxa, only a subset of habitats where the juveniles may be found ("juvenile habitats"), will actually produce a greater than average amount of recruits per unit area which will actually contribute to adult assemblages. Such habitats display a greater "nursery value", that is to say provide a greater contribution to adult populations than the average contribution of all juvenile habitats from any combination of four factors: density, growth, survival of juveniles and their capacity to move toward and reach adult habitats. These habitats therefore have a "nursery role" (Beck et al., 2001; Heck et al., 2003).

Some factors may contribute to variation in nursery value between habitats or between sites for a given habitat: notably, initial density of settlers, which is mainly influenced by adult spawning event intensity and subsequent pelagic dispersion of eggs and larvae according to oceanographic currents (Basterretxea et al., 2012a). At a local scale, assuming that each habitat in a given site receives the same initial input of settlers from the pelagos, patterns of juvenile densities across habitats will be shaped by active habitat choice or differential mortality (Savino and Stein, 1989). Both of them are mediated by habitat quality (Hindell et al., 2000) in terms of food availability and predation rates, which in turn are shaped by habitat tri-dimensional structure: "complex" habitats –*sensu* August (1983)- provide better refuges against predation and more food, which facilitates rapid growth and consequently reduce predation risk according to the stage-duration hypothesis (Vigliola, 1998). A habitat displaying high densities, growth and survival of juveniles will ultimately require a good connectivity with adult habitats to contribute to adult population replenishment. Only in such cases will this habitat truly have a higher than average nursery value and therefore play a nursery role (Beck et al., 2001). Nevetheless, many studies used juvenile densities alone as a proxy of habitat nursery value.

The paradox of coastal areas lies in the fact that they display many nursery habitats, essential for assemblages replenishment (Harmelin-Vivien et al., 1995) while they also concentrate human-induced impacts leading to (1) habitat transformations with modification of their tri-dimensional structure (Coll et al., 2010; Francour et al., 1999; Guidetti et al., 2003; Levi and Francour, 2004) and (2) potential disturbances of connectivity between essential habitats (Thompson et al., 2009). Both consequences may reduce habitats' nursery value through the processes explained before and therefore threat coastal habitats nursery role and the replenishment of coastal fish assemblages. Given such paradoxal situation, nursery habitats have been considered as key units of the seascapes that must be taken into account in the design of coastal areas management priorities. However, little have been done to put this into practice. Such habitat-focused management strategies have been encouraged by legislative measures, such as the Habitat European Directive (92/43/EEC) but up to now, in the best cases, it led to mostly mono-habitat-focused protections, without taking into account a multi-specific and connectivity perspective. In tropical seas, efforts have been done in that direction: for instance, the

community-based co-management approach of Mohéli Marine Park (Comoros, Indian Ocean) (Granek and Brown, 2005) was designed based on the cartography of essential habitats for various taxa (marine mammals, turtle feeding grounds, fish nursery grounds) (David et al., 2003) and of essential ecosystem services provided by habitats (e.g. coastal erosion protection) (David and Mirault, 2009). In Mayotte Island (Indian Ocean), the selection of Ramsar wetland sites focused on essential habitats for various taxa of fishes and birds, taking the spatial partition of various species into various habitats into account (seagrass meadows, mangroves) (Cheminée, 2002; Direction de l'Agriculture de Mayotte et al., 2002). Contrastingly, in the Mediterranean, although infralittoral habitats are much narrower than in many tropical areas, such approaches are mostly lacking and only in some regulations, a mono-species-focused approach may exist (e.g. for *Merlucius merluccius*). Nevertheless, the development of such "seascape approach" is actually considered in the current legal framework and, for example, the French National Parks administration recently developed similar guidelines with continental examples (INEA et al., 2009; Thompson et al., 2009). Its application to marine habitats requires more detailed knowledge on essential habitats, especially nurseries.

In the Mediterranean Infralittoral, nursery habitats for some species have already been described: the shallow and sheltered, gently sloping bottoms of blocks and pebbles have a higher than average nursery value for *Diplodus* spp. (*D. puntazzo*, *D. vulgaris*, *D. sargus*, *D. cervinus*) (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). Indeed, it has been shown that these habitats display higher densities of juveniles (Harmelin-Vivien et al., 1995), with higher growth and survival rates (Vigliola, 1998), and that they are well connected with adult distant habitats (recruits migration abilities) (Di Franco et al., 2012). Previous studies showed that macrophytes-formed habitats, namely seagrass meadows (*Posidonia oceanica*, *Cymodocea nodosa*) host higher densities of fish juveniles than other neighboring habitats (Guidetti, 2000; Guidetti and Bussotti, 1997; Guidetti and Bussotti, 2000) and highlighted the likely nursery role of these meadows. This role has been in part attributed to *Posidonia oceanica* high tri-dimensional complexity (Francour, 1999; Francour and Le Direac'h, 2001). Among the rocky infralittoral level, other photophilic macrophyte-formed habitats are covering large proportions of the bottoms and might have a nursery role, although this was not precisely quantified previously. Canopy forming, erect macroalgal assemblages (i.e. erect Multicellular Photosynthetic Organisms belonging to the Chlorobionta, Rhodobionta and Phaeophycea) can form wide arborescent forests (Ballesteros, 1992; Giakoumi et al., 2011; Sala et al., 2012; Sales and Ballesteros, 2010; Verlaque, 1987) (Fig. 1). In the "Natura 2000" framework, they are referred as Habitat of community interest subtype "Reef, n°1170-13" (http://www.ecologie.gouv.fr). Some studies showed that fish juvenile abundances, namely Labridae species, were positively correlated with the cover of erect macroalgal assemblages on rocky bottoms (Garcia-Rubies and Macpherson, 1995; Letourneur et al., 2003; Macpherson and Raventos, 2005; Macpherson

and Zika, 1999; Raventos and Macpherson, 2001; 2005a; b). More particularly some rare studies suggested the potential nursery role of the complex, canopy forming *Cystoseira* spp. forests (Fucales, Chromobiontes, Stramenopiles) (Riccato et al., 2009) but their nursery value has never been quantitatively measured or estimated.

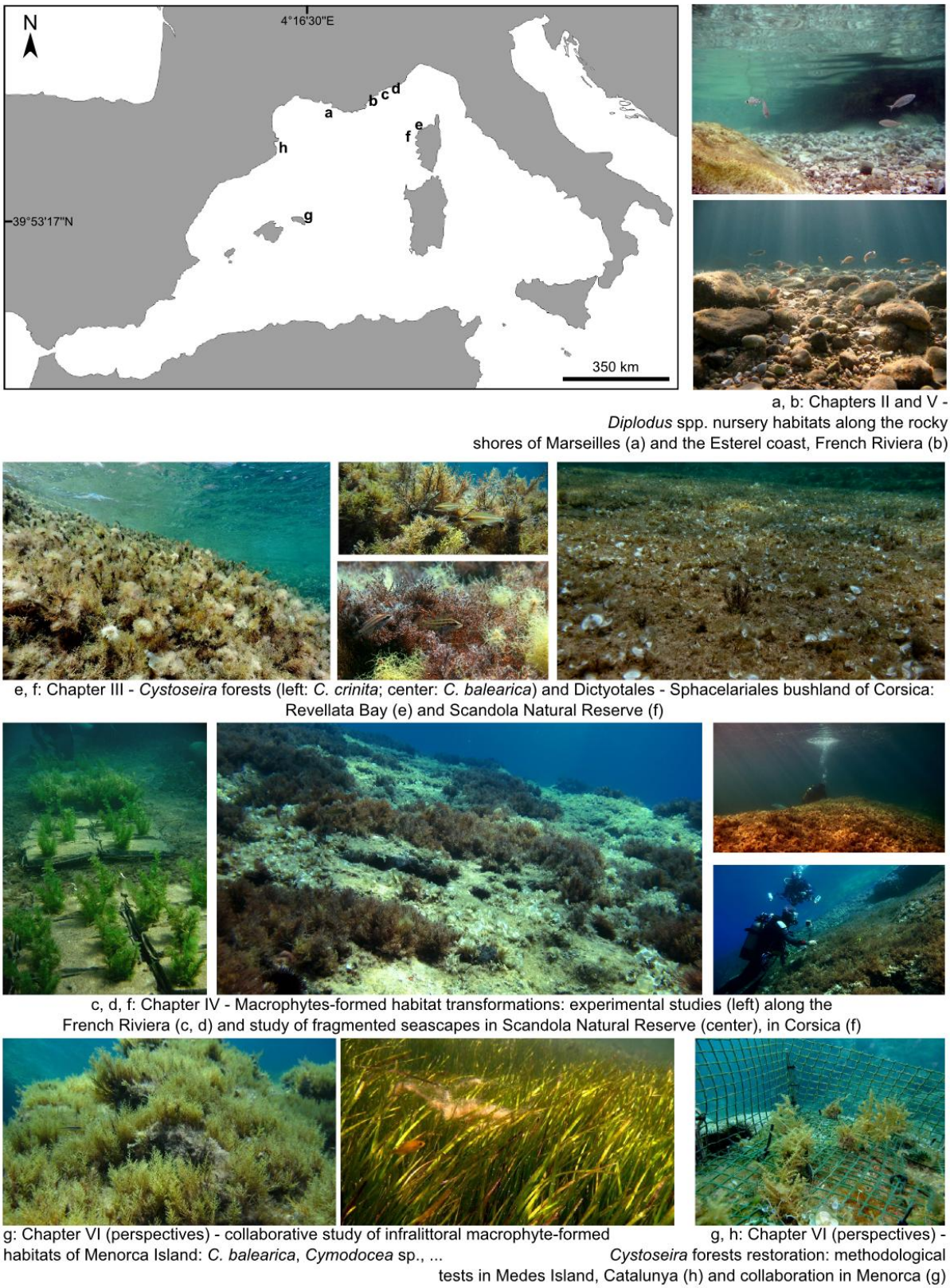
Assessing *Cystoseira* forests nursery value is a priority since these forests have been reported to dramatically regress in many Mediterranean locales where they used to be the dominant and habitat forming species of rocky infralittoral (Thibaut et al., 2005), sheltering high biodiversity and biomass (Ballesteros et al., 1999). Factors explaining such habitat transformations include human trampling (Milazzo et al., 2004a), chemical pollution (Sales and Ballesteros, 2009), dominance by introduced invasive species (Verlaque, 1994), overfishing of sea-urchin predators (mainly Sparidae and Labridae) and subsequent overgrazing by sea urchins (trophic cascade) (Sala et al., 1998), or overgrazing by introduced invasive fish species (such as *Siganus* spp.) (Sala et al., 2011). *Cystoseira* forests regression implies notably canopy cover density decrease, forest fragmentation and patch-size reduction (Ballesteros et al., 2010; Ballesteros et al., 2002). Some opportunistic fast growing assemblages, such as the bush-like Dictyotales and Sphacelariales may occupy patches cleared from the *Cystoseira* canopy cover. Ultimately, the complex, arborescent strata may be fully replaced by other, less complex alternate stable states of the biocenosis of photophilic macrophytes of the Infralittoral: a regime shift, due for example to trophic cascades, may cause the total loss of the arborescent strata, turning the habitat into barren-grounds; i.e. overgrazed state with sea-urchins and Corallinales. An alternate state may be formed by the opportunistic species *Padina pavonica* or *Halopteris scoparia* creating a shrubby assemblage (Dictyotales and Sphacelariales (DS) bushland) (Bonaviri et al., 2011; Hereu, 2004). While the switch from forest to barrens is fast, the natural restoration of forest may be very slow (Soltan et al., 2001) due notably to the low dispersal capacities of *Cystoseira* species (Susini et al., 2007), even if initial causes of forest regression are removed.

In order to provide managers with useful data on functionally essential habitats, it is necessary to better know the relative nursery value of Mediterranean infralittoral habitats, especially *Cystoseira* forests, and how it may vary through space. Besides, for a given habitat, the impacts of habitat transformations on its nursery value must be assessed: how much productivity is lost for the replenishment of coastal fish assemblages and fisheries? Furthermore, it is also necessary to know the spatial distribution and abundance of each of these various essential habitats along the shores. Finally, it is important to assess if current management strategies do take essential habitats spatial distribution and connectivity into account. During my PhD thesis I focused more particularly on the rocky Mediterranean Infralittoral, according to the following plan; corresponding studied localities and habitats are given in Fig. 1.

1.2 Main questions and objectives

- Is a given habitat whose nursery role is recognized (*Diplodus* spp. nurseries) common along the rocky shores and does it display homogenous densities of juveniles? **(Chapter II)**
- What is the relative nursery value of various macrophyte-formed habitats displaying different tri-dimensional structure, notably *Cystoseira* forests and Dictyotales-Sphacelariales bushland, among other habitats of the Infralittoral seascape mosaic? **(Chapters III-2 and III-4)**
- How much does the nursery value of a given habitat (notably *Cystoseira* forest) vary through space and how much is this variability related to habitat tri-dimensional structure characteristics? **(Chapter III-3)**
- More generally, which may be the involved underlying processes shaping juvenile density patterns across *Cystoseira* forests and Dictyotales-Sphacelariales assemblages? **(Chapter III-5)**
- Consequently, what are the impacts of anthropogenic habitat transformations on their nursery value, notably in the case of *Cystoseira* forests? **(Chapter IV)**
- Finally, does the spatial design of current management measures take the spatial distribution and connectivity of essential habitats, notably nurseries, into account? **(Chapter V)**

Chapters II, **III** and **IV** aim at contributing to the identification within the Mediterranean infralittoral seascape mosaic, of the habitats and sites within habitats that play a nursery role, in order to improve the focus of conservation efforts. **Chapter V** gives a conceptual framework to help managers incorporate these data into coastal management planning at the scale of the full seascape. **Chapter VI** gives a discussion of the main results and some perspectives. **Chapter VII** details the valorization of the PhD works (papers, conferences, lectures, vulgarization).



a, b: Chapters II and V - *Diplodus* spp. nursery habitats along the rocky shores of Marseilles (a) and the Esterel coast, French Riviera (b)

e, f: Chapter III - *Cystoseira* forests (left: *C. crinita*; center: *C. balearica*) and Dictyotales - Sphacelariales bushland of Corsica: Revellata Bay (e) and Scandola Natural Reserve (f)

c, d, f: Chapter IV - Macrophytes-formed habitat transformations: experimental studies (left) along the French Riviera (c, d) and study of fragmented seascapes in Scandola Natural Reserve (center), in Corsica (f)

g: Chapter VI (perspectives) - collaborative study of infralittoral macrophyte-formed habitats of Menorca Island: *C. balearica*, *Cymodocea* sp., ...

g, h: Chapter VI (perspectives) - *Cystoseira* forests restoration: methodological tests in Medes Island, Catalunya (h) and collaboration in Menorca (g)

Fig. 1: The North-Western Mediterranean, studied localities (lower characters from a to h), corresponding chapters (II to VI) and habitats (pictures); detailed descriptions of each habitat are given in each corresponding chapter. Photos: A. Cheminée, E. Vidal and A. Cuadros-Casado.

1.3 Introduction (French translation)

Dans le but de fournir aux gestionnaires du littoral des données relatives aux habitats ayant un rôle essentiel à certaines étapes clef du cycle de vie des poissons (Téléostéens), il est plus particulièrement nécessaire de mieux comprendre la valeur relative de nourricerie - *sensu* Beck et al. (2001) – des différents habitats infralittoraux Méditerranéens. Les forêts de Cystoseires (Fucales, Chromobiontes, Stramenopiles), en forte régression (Thibaut et al., 2005), méritent une attention particulière. De plus, pour un habitat donné, la variabilité spatiale de sa valeur de nourricerie et les conséquences de ses transformations sur celle-ci doivent être estimées. Par ailleurs, il est également primordial de connaitre la distribution spatiale et la quantité disponible de chacun de ces habitats clefs le long des côtes. Enfin, il est important d'estimer si le design actuel des mesures de gestion prend en compte la distribution spatiale des habitats essentiels et leur connectivité. Au cours de cette thèse, je me suis plus particulièrement intéressé aux habitats de l'Infralittoral rocheux, selon le plan présenté ci-après. Les habitats et localités correspondantes sont indiqués en Fig. 1. **Chapitre II** : pour un habitat dont le rôle de nourricerie est établi, i.e. les nourriceries des *Diplodus* spp. (Harmelin-Vivien et al., 1995), est-il commun le long des côtes rocheuses et présente-t-il des densités de juvéniles constantes dans l'espace ? **Chapitre III-2 et III-4** : au sein de la mosaïque d'habitats de l'Infralittoral, quelle est la valeur relative de nourricerie d'habitats à macrophytes présentant des structures tridimensionnelles différentes, notamment les forêts de Cystoseires et les brousses à Dictyotales-Sphacelariales ? **Chapitre III-3** : quelle est la variabilité spatiale de la valeur de nourricerie d'un habitat donné et à quel point est-elle liée aux caractéristiques structurelles de l'habitat ? **Chapitre III-5** : plus généralement, quels sont les processus sous-jacents pouvant expliquer les patrons d'abondance des juvéniles de poissons au sein des forêts de Cystoseires et des brousses à Dictyotales-Sphacelariales ? **Chapitre IV** : en conséquence, quels sont les impacts des transformations des habitats sur leur valeur de nourricerie, notamment dans le cas des forêts de Cystoseires ? **Chapitre V** : enfin, le design spatial des mesures de gestion côtière prend-t-il en compte la distribution des habitats essentiels et leur connectivité ?

Les **chapitres II, III,** et **IV** contribuent à l'identification au sein de la mosaïque de l'Infralittoral Méditerranéen des habitats et sites jouant un rôle de nourricerie pour les juvéniles de poissons, afin d'ajuster les efforts de conservation. Le **chapitre V** propose un cadre conceptuel aidant les gestionnaires à incorporer ces données dans une approche de la gestion côtière à l'échelle des paysages sous-marins. Le **chapitre VI** discute les principaux résultats et donne quelques perspectives. Le **chapitre VII** présente en annexe les outils mis en œuvre afin de valoriser les travaux de cette thèse.

Chapter II. State of known nurseries along rocky shores

Villefranche Bay, 15th of June 2009 (-0.5 meter). Shallow, gently sloping bottoms with heterogeneous rocky substratum made of pebbles, boulders and blocks are nursery habitats for various Sparidae species. Notably, *Diplodus puntazzo*, *D. vulgaris* and *D. sargus* (one ~25-30 mm TL individual on the left of the picture) show a temporal partitioning of their settlement in these nurseries from October to June.

Chapter II. State of known nurseries along rocky shores

2.1 Chapter introduction

In the Mediterranean, fishes from the Sparidae family include species of both important ecological and economical importance. Both recreational and professional fisheries are targeting species belonging e.g. to the genus *Diplodus*, *Sparus*, *Dentex* or *Pagrus* (Claudet et al., 2010; Guidetti et al., 2008). *Diplodus sargus* for example is one of the most abundant taxa affected by competition spear fishing in the Balearic Islands (Coll et al., 2004). For *Diplodus* species, juveniles have strict and well described micro-habitat requirements: more specifically *D. sargus*, *D. vulgaris*, *D. puntazzo*, and *D. cervinus* nursery habitat are characterized by shallow, gently sloping bottoms with heterogeneous rocky substratum, situated along shores not exposed to strong hydrodynamism (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). For such species whose nursery habitats are well described, coastal managers still require for each zone under their jurisdiction a detailed analysis of these nurseries : for a given shoreline, where are located the *Diplodus* nursery grounds? Indeed, cartographies of the biocenosis, performed e.g. in the frame of the Habitats European Directive in “Natura 2000” sites, do not provide a sufficiently detailed description of micro-habitats in order to locate these nurseries. Besides, which proportion of the coastline do these nurseries represent, i.e. are they common along the coast? Finally, do they display homogeneous abundances of juveniles, i.e. is their nursery value –sensu Beck et al (2001)- constant through space? These three types of information will be essential for managers in order to perform adequate choices for coastal development programs and fisheries management.

In this Chapter, I present two papers contributing to answer these questions in two different rocky shore localities along the South-East coast of France: the Calanques National Park near Marseilles city and the Cap Roux no-take zone along the “Esterel” coast (see Fig. 1 in Chapter I). These localities share some common features: both are marine protected areas, characterized by rocky shores displaying abrupt, deep and exposed coast interspersed with small protected coves displaying shallower gently sloping rocky bottoms. Both areas are quite pristine but located near heavily human impacted shorelines (respectively the bay of Marseilles and the Gulfs of Frejus and la Napoule-Cannes city). They both host active professional and recreational fisheries (Morat et al., 2011; Seytre and Francour, 2009).

- Part 2.2: I prepared a **first paper (Cheminée et al., 2011)** based on data I gathered during my Master thesis in 2004 in Marseilles University, in collaboration with the public organization (the "GIP Calanques") in charge of coastal management of the local "Calanques" 52 km rocky shoreline. From January to June 2004, after a preliminary cartography of micro-habitats, I selected various *Diplodus* nurseries where I undertook visual census of *Diplodus* settler assemblages weekly: a total of 90 censuses were performed to study the temporal trends of settling and juvenile growth for two species (*D. puntazzo* and *D. vulgaris*) (Cheminée, unpublished data). During my PhD, I re-analyzed these data, leading to the present paper which aimed at (i) locating and (ii) quantifying *Diplodus* nursery habitats and (iii) estimating the amount of settlers that settled during the winter and spring of 2004 in the nurseries located along the rocky shore of Marseilles. It is worth mentioning that during this research, this rocky shore was designated in 2012 as a National Park covering the terrestrial and marine part of the studied locality.

- Part 2.3: I participated in the **second paper (Arceo et al., 2012)** done within the frame of Hazel Arceo's PhD thesis (Arceo, 2012). The objective of this study was to determine the effects of protection (Cap Roux MPA) on *Diplodus* juvenile density and mortality at a local scale along the "Esterel" rocky shore. My contribution was the transfer of the methodology I used for the paper previously mentioned (Cheminée et al., 2011) to H. Arceo: notably we performed together in December 2009 a preliminary micro-habitat survey along the rocky shore of the Esterel and Cap Roux MPA. From this micro-habitats survey we selected the *Diplodus* nursery sites used for the second paper. During the summer 2010 we performed together a first set of *in situ* juvenile underwater visual census (UVC, snorkeling), applying the same methodology I used in Cheminée et al. (2011). I also made inputs during the writing of the paper (Arceo et al., 2012).

2.2 Paper: Assessment of Diplodus *spp. (Sparidae) nursery grounds along Marseilles rocky shores (France, NW Mediterranean)*

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Assessment of *Diplodus* spp. (Sparidae) nursery grounds along the rocky shore of Marseilles (France, NW Mediterranean)

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SUMMARY: This work aimed at performing a large scale assessment of *Diplodus* spp. (Sparidae) nurseries along the rocky shore of Marseilles (France, NW Mediterranean) by locating and quantifying nursery microhabitats and estimating the settlement pattern along this shore in 2004. Nursery grounds of *Diplodus* spp. represented only 9% of the 52 km-long rocky shore of Marseilles. Their location, shallow rocky habitats sheltered within coves, made them vulnerable to human-induced habitat transformations. *D. vulgaris* settled along this coast at the end of February 2004 and *D. puntazzo* settled a couple of months earlier. Maximum densities observed reached 215 and 67 ind./100 m for *D. vulgaris* and *D. puntazzo* respectively. The settlement rates were spatially variable. At a regional scale, lower settlement rates were observed within the south and centre zones, compared to those observed in the west, east, and the Marseilles Bay zones. Suitable nurseries along this shore seem insufficient for the replenishment of adult assemblages, which suggests that they depend on the migration of adults from other areas. Along the Marseilles rocky shore, coastal development projects leading to the destruction of habitats would represent a major threat to the *Diplodus* life cycle, which could be even greater than usual given the vulnerability and small size of the nurseries. These results show that it is necessary to protect these scarce local nursery habitats and manage other nearby nurseries to ensure the survival of fish at a critical life stage and the replenishment of adult assemblages.

Keywords: *Diplodus*, nursery microhabitats, settlement, settlers, juveniles, shallow rocky habitat, habitat transformation, coastal zone management.

RESUMEN: Evaluación de los sitios de asentamiento de *Diplodus* spp. (Sparidae) a lo largo de la costa rocosa de Marsella (Francia, Mediterráneo Noroccidental). – Este estudio tiene por objetivo realizar una evaluación a gran escala de las áreas adecuadas para el asentamiento de *Diplodus* spp. a lo largo de la costa rocosa de Marsella (Francia, Mediterráneo Noroccidental) a través del estudio de la ubicación y abundancia de estos microhábitats y del patrón de asentamiento durante el año 2004. Los microhábitats de asentamiento representaron tan sólo el 9% de los 52 km de las extensas costas rocosas de Marsella. Su ubicación en el interior de las calas, en substratos rocosos protegidos y a poca profundidad, los convierte en hábitats vulnerables a las transformaciones inducidas por el hombre. El asentamiento a lo largo de esta costa tuvo lugar a finales de febrero 2004 para *D. vulgaris*, y dos de meses antes para *D. puntazzo*. Las máximas densidades observadas por cada 100 metros de costa alcanzaron 215 y 67 individuos de D. vulgaris y *D. puntazzo* respectivamente. Las tasas de asentamiento fueron variables en el espacio. A escala regional, las tasas de asentamiento menores fueron observadas en las zonas sur y central. Los lugares de asentamiento adecuados a lo largo de esta costa parecieron insuficientes para abastecer las poblaciones adultas, lo que sugiere que éstas dependen de la migración de adultos desde otras áreas. La urbanización de la costa produciría destrucción de estos microhábitats, lo que pondría en peligro el ciclo vital de *Diplodus,* dada la vulnerabilidad y rareza de dichos microhábitats. Nuestros resultados mostraron la necesidad de proteger estos escasos hábitats de asentamiento y gestionar zonas de asentamiento a su alrededor para asegurar la conectividad entre hábitats, la supervivencia de determinadas fases críticas de los peces y el suministro de individuos a las poblaciones adultas.

Palabras clave: *Diplodus*, asentamiento, juveniles, hábitats rocosos, transformación de hábitats, gestión de áreas costeras.

INTRODUCTION

Benthic and nektobenthic fish have a bipartite life cycle (Vigliola, 1998), with a pelagic larval phase and a more sedentary and benthic adult phase. In our study, settlement is defined as the arrival of early juvenile fish (referred to as "settlers") to benthic nursery areas after their pelagic larval phase. Recruitment corresponds to the later incorporation of these juvenile fish into adult populations after their settlement and survival in nurseries (referred to as "recruits") (Levin, 1994; Macpherson, 1998). "Juvenile" is used as a broader term that encompasses both settlers and recruits. The settlement rate can be defined as the number of new individuals joining the benthic habitat for a given nursery area. The recruitment level can be defined as the number of settlers remaining at the end of the post-settlement period, that is, those who survived and who will actually join adult assemblages (Macpherson, 1998).

The transition between pelagic and benthic stages is a key point of the species' life cycle (Brothers and MacFarland, 1981). Factors affecting the settlement and recruitment processes determine the renewal of populations and shape the structure of adult assemblages (Sano, 1997). To conserve marine resources, it is therefore a priority to study the factors affecting these processes. Among these, larval dispersion modalities (i.e. settler supply) and nursery habitat availability are key factors. Microhabitats are defined as subsets of biotic and abiotic habitat components; i.e. small-scale differences in habitat features which produce small-scale patchiness and different microhabitats within a few square meters (Chapman, 1995). Nurseries are defined as specific microhabitats whose characteristics are favorable for fish settlement. The characteristics of microhabitats appear to be a determining factor for settlement and recruitment success because settlers often have strict microhabitat requirements, as shown for sparids in the NW Mediterranean (Francour and Le Direac'h, 1994; García-Rubíes and Macpherson, 1995; Harmelin-Vivien *et al*., 1995; Guidetti and Bussotti, 1997; Le Direac'h and Francour, 1998; MacPherson, 1998; Vigliola *et al*., 1998; Planes *et al.*, 1999). Other published data also provide information on microhabitat requirements for settlement of Blenniidae (Macpherson and Zika, 1999; Macpherson and Raventos, 2005), Labridae (García-Rubies and Macpherson, 1995; Raventos and Macpherson, 2005a, b), Pomacentridae (García-Rubies and Macpherson, 1995; Macpherson and Raventos, 2005), Serranidae and Mullidae (García-Rubies and Macpherson, 1995).

Nursery microhabitats, where the pelagic-benthic transition can occur, are thus key habitats. Their availability, structure and composition are essential for fish settlement and recruitment. A persistent concern in coastal management is that coastlines have nursery habitats for fish species but are greatly disturbed due to the direct impacts of human activities (Ballesteros, 2009). As a consequence, the species' life cycle and the conservation of adult assemblages may be affected if key habitats for juvenile fish settlement are transformed or destroyed (Harmelin-Vivien *et al*., 1995). In order to ensure conservation of fish assemblages, coastal management should focus on conserving these specific nursery habitats. Thus, scientific assessment must provide information on (i) the availability of these microhabitats (location, abundance), (ii) their larval supply (settlement rates), and (iii) the survival of settlers (recruitment level). Furthermore, it is also important to estimate the consequences of these key habitat transformations.

Previous studies, mainly performed in the NW Mediterranean, generally focused on microhabitats at a local scale, e.g. specific coves, and studied their intrinsic ecological functions. However, the availability of nurseries and settler supply patterns along the coast at a larger scale for a given area has never previously been assessed. We conducted a large-scale assessment of some Sparidae nurseries along the Marseilles 52 km-long rocky shore (NW Mediterranean, France). The Common two-banded seabream *Diplodus vulgaris* (Geoffroy Saint-Hilaire, 1817) and the Sharpsnout seabream *D. puntazzo* (Cetti, 1777) were chosen due to their high abundance, commercial value, and because their modalities of settlement and recruitment on shallow rocky bottoms are well described (e.g. García-Rubies and Macpherson, 1995; Harmelin-Vivien *et al*., 1995). The sea breams *D. vulgaris* and *D. puntazzo* are well-known target fish for commercial and sport fisheries in the western Mediterranean. Adults are found between 0 and 150 m on rocky, sandy and seagrass bottoms. *D. vulgaris* forms small to large schools, while *D. puntazzo* is more solitary. Settlement takes place after a 15-30 day pelagic egg and larval phase (Vigliola, 1998) following reproduction events by adults in deep habitats. Settlers of both species are gregarious and share the same nursery grounds, usually located in shallow (less than 2 m deep) sheltered areas, with gently sloping substrates of gravel, pebbles, or boulders (Harmelin-Vivien *et al*., 1995). *D. puntazzo* settles in October-November, while settlers of *D. vulgaris* generally arrive in two settlement pulses, early November and January. Both species start to leave nursery grounds (recruitment) in May-June (Macpherson, 1998; Vigliola, 1998).

In order to perform a large scale assessment of the nurseries on the Marseilles rocky shore, we tested whether nurseries are common along the rocky shore and if they have homogenous abundances of settlers. Thus, this work aimed at (i) locating and (ii) quantifying *Diplodus* nursery grounds (microhabitat availability), and (iii) estimating the amount of settlers that settled during the winter and spring of 2004 (settlement rates) along this shore.

MATERIALS AND METHODS

Study area

Between January and May 2004, *Diplodus* nursery grounds were investigated at a regional scale at 23

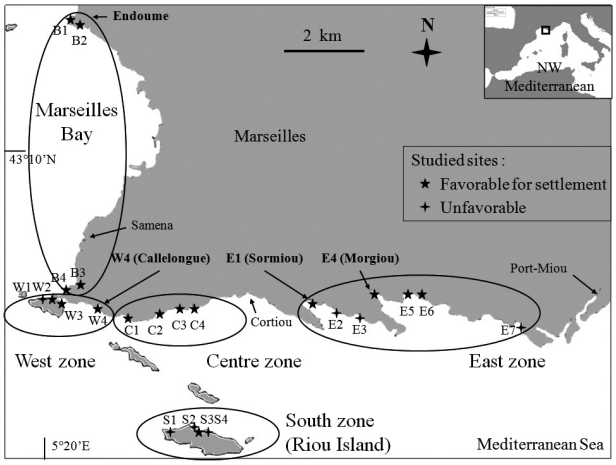

FIG. 1. – Study area: Marseilles Bay and the rocky shore; boundaries of the rocky shoreline: Samena and Port-Miou coves; five studied zones for the large scale study (bay, west, centre, south, east) representing a total of twenty three studied sites (favorable (stars) and unfavorable (crosses) sites for *Diplodus* settlement); three detailed study sites (Calanques) for the local scale study: E4 (Morgiou), E1 (Sormiou), W4 (Callelongue); Cortiou sewage.

randomly selected sites along the Marseilles Bay and along the 52 km-long rocky shore of Marseilles, from Samena cove to Port-Miou cove, including the Riou archipelago (Fig. 1). According to previous knowledge of *Diplodus* spp. nursery grounds (Harmelin-Vivien *et al*., 1995), among these 23 sites, 16 sites could be considered *a priori* as favorable and 7 as unfavorable for settlement. There were geomorphologic differences along the bay and rocky shore, and sites were grouped into five distinct zones (Marseilles Bay, west, centre, south, and east; Fig. 1). The east zone (E) contained large wide coves open towards the south-east. The centre zone (C) contained small, narrow, south-west oriented coves. The south zone (S) corresponded to the Riou archipelago, located at 1.8 nautical miles southward from the rocky shore. The west zone (W) was characterized by its intermediate position between the rocky shore and Marseilles Bay. Marseilles Bay (B) encompassed sites located within this large bay which was oriented westward. In order to complete the regional large scale study, a more detailed and extensive study was performed on a local scale in three of the sixteen favorable nursery sites of the rocky shore (coves termed "Calanques"; Fig. 1): Callelongue (site W4), Sormiou (site E1) and Morgiou (site E4).

Location and quantification of nursery grounds

The first step for assessing nurseries of this shore consisted in locating and quantifying favorable microhabitats for settlement, i.e. potentially suitable nursery grounds for settling *Diplodus*. Consequently, detailed mapping was first performed at sites W4, E1 and E4 (Fig. 1). This first mapping is referred to hereafter as local scale mapping. At the scale of each of these three Calanques, since we knew that nurseries would be found in a range of shallow waters (see ref. above), we mapped microhabitats within shallow depths (0-3 m). Mapping was carried out in situ, during one week in January 2004, by one single observer snorkeling along the entire shoreline of each of the three Calanques. The depth, slope, substratum type, biotic cover and exposure of the microhabitats of the superficial part of the infralittoral zone were recorded using the methodology previously described by Harmelin-Vivien *et al*. (1995). The location of the nursery grounds within these Calanques was then deduced and placed on the maps by comparing the recorded microhabitat characteristics with the previously described characteristics of *Diplodus* nursery grounds (Harmelin-Vivien *et al*., 1995). Then, at the regional scale, i.e. along the Marseilles Bay and the 52 km long rocky shoreline, we deduced the location of all other possible nurseries by analyzing topographic and geomorphologic maps. During the second phase of the study, in April 2004 (see next section), these deductions were validated by in situ snorkeling observations, as previously described. The total rocky shoreline and its portion of shoreline favorable for settlers were then measured with the help of a topographic map, ground truthed with field measurements. Thus, the proportion of the rocky shoreline favorable for settlement, and therefore acting as nursery grounds, was calculated.

Quantification of *Diplodus* spp. settlers

Once nursery grounds were located and quantified, their settler assemblages for 2004 were quantified. For a given year, settler density measured in situ can be used as an indicator of the settlement rate for a given area. The settler density refers to the amount of settlers counted for a given unit of shoreline length. For the local scale study (sites W4, E1, E4), three nursery replicates per Calanque were randomly chosen among those previously identified during the local scale mapping. (referred to as a, b, c; Fig. 2). In each nursery, *Diplodus* settler assemblages were censused weekly from 27 February to 14 May 2004. A total of 90 censuses were performed to study the temporal trends of settling for these two species (Cheminée, unpublished data). The maximum density observed for each replicate over this time frame was used as a measure of the settlement rate for the year 2004 (present study).

At the regional scale, large scale quantification of the 2004 settlement event was carried out by assessing the 23 sites along Marseilles Bay and the rocky shore (Fig. 1). *Diplodus* settler assemblages were censused in all 23 sites on the same date, between 21 and 23 April, 2004. Replicated counts were carried out at each site. A total of 79 censuses were performed, taking both species into account. The average density of each species observed for each of the 23 sites at this specific time was taken as a measure of the settlement rate for the year 2004 and used to assess the regional settlement pattern.

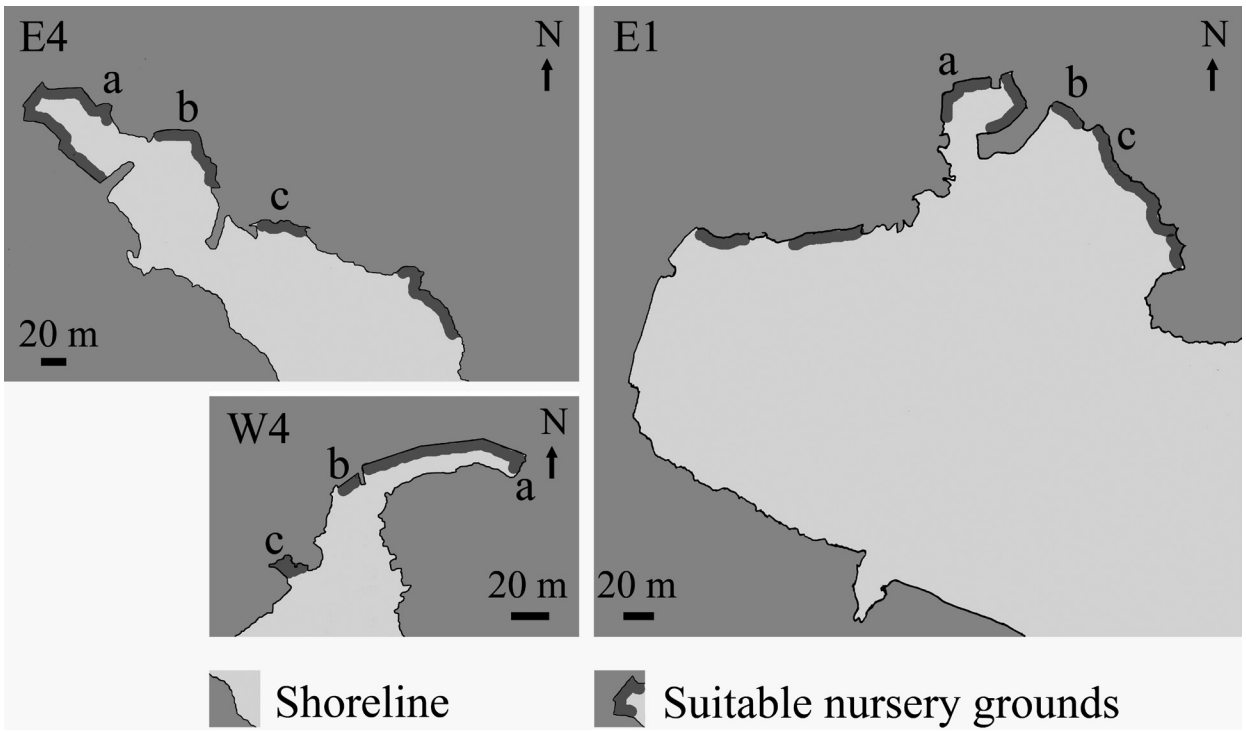

FIG. 2. – Shaded areas represent the location of suitable microhabitats for *Diplodus* settlers (nursery grounds) in the three studied Calanques; E4 = Morgiou; E1 = Sormiou; W4 = Callelongue; Labels (a, b, c) indicate the three monitored nursery replicates in each Calanque.

For both local (i.e. within the 3 Calanques) and regional (the 23 sites along the shoreline) scales, *Diplodus* settler assemblages were monitored by an Underwater Visual Census (UVC). Within each site, snorkeling at the same time of day (between 11 am and 3 pm), the diver swam slowly along the shoreline of the entire area. When individuals or groups of settlers were observed, the abundance and size of each species were recorded on a plastic slate. The total length (TL) of individuals was estimated with the help of fish silhouettes of different sizes pictured on the slate (5 mm size classes). Thanks to its spatial configuration, each nursery was sampled completely by swimming parallel to the shoreline along a predetermined 5 meter-wide transect. Since nurseries were separated from each other by abrupt, unfavorable edges that would impede the circulation of settlers, each nursery and corresponding counts were independent from each other. Slow swimming helps to prevent the dispersal of settlers and allows them to be counted and their sizes estimated (Harmelin-Vivien *et al*., 1985, 1995; Vigliola *et al*., 1998). Macpherson (1998) evaluated the precision of this size estimating method as +/- 3.5 mm for *Diplodus* species. For the local scale study, within the three Calanques, where accurate maps of nurseries were obtained, counts were standardized according to length unit (density / length of shoreline). However, for the regional, large scale study, counts were standardized according to time unit and expressed as average settler density per 10 minute count. At the regional scale, during our censuses, we recorded the microhabitat characteristics of each site in situ using the same criteria as previously described (Harmelin-Vivien *et al*., 1995).

Data analysis

The normality assumption of density data was tested with the Levene test. Homogeneity of variances was tested with the Kolmogorov-Smirnov test. If tests were negative, data were log transformed [log (1+x)] or square root transformed. If not satisfactory, the Kruskal-Wallis or Mann-Whitney non-parametric test was used. At the local scale, mean maximum densities of settlers observed in each of the three Calanques (W4, E1, E4) were compared among Calanques or among species using a Kruskal-Wallis non-parametric test. The independent variable was either the Calanque (3-factor levels for each species) or the species (2-factor levels), while the dependant variable was the maximum density per nursery replicate for the considered species. At the regional scale, to study settlement patterns along the shoreline, the 23 sites surveyed were pooled according to their geographic position into the 5 zones previously described: east, central, south, west and Marseilles Bay (Fig. 1). The variability of *Diplodus* settler density recorded on a single date was studied with a Kruskal-Wallis test and a Student-Newman-Keuls post-hoc test, which is a pair wise comparison test used after the Kruskal-Wallis test to assess differences among groups. The independent variable was the zone (5-factor levels) and the dependant variable was the density for each site and species.

TABLE 1. – Maximum densities of settlers observed for *Diplodus puntazzo* and *Diplodus vulgaris* in the monitored nursery replicates (ind./100 m) and means within the local scale study sites (Calanques); SE, Standard error; CV, coefficient of variation.

Site (Calanque)	Replicate	*D. puntazzo*	Mean±SE (CV)	*D. vulgaris*	Mean±SE (CV)
E4 (Morgiou)	E4-a	39.6	29.3±5.1 (30)	54.9	49.0±6.8 (24)
	E4-b	24.8		56.7	
	E4-c	23.6		35.4	
E1 (Sormiou)	E1-a	14.4		47.6	
	E1-b	37.1	23.8±6.8 (50)	214.8	113.4±51.4 (76)
	E1-c	20.0		77.8	
	W4-a	4.7		12.2	
W4 (Callelongue)	W4-b	20.1	21.3±9.9 (81)	100.3	73.9±31.0 (73)
	W4-c	39.1		109.4	
E4, E1, W4 pooled			24.8±4 (48)		78.8±19.8 (75)

The local and the regional settler quantification used two different parameters and corresponding units: maximum densities observed during the monitored time frame vs. densities observed for a given date; abundances per shoreline length and abundances per 10 min. count. In the first case we aimed at quantifying the maximum hosting capacity of nurseries for this year, while in the second case we aimed at comparing the settlement rates among zones along the shoreline. For this second aim, recording densities in April allowed us to obtain an integrated measurement of the settlement event for this year because by this time the main settlement pulses were supposed to have occurred and to be pooled in the settler assemblages now present in nurseries.

RESULTS

Location and quantification of nursery grounds

At the scale of each of the three selected Calanques, nurseries were always located in the innermost part of each Calanque; Figure 2 gives their exact location.

Among the 23 sites surveyed along the bay and the rocky shore, all 16 *a priori* favorable sites had settlers, and all 7 *a priori* unfavorable sites did not have settlers. Along the total rocky shoreline, these field censuses allowed us to ground truth 3.1 km of *a priori* favorable shoreline for settlement over a total amount of *a priori* favorable shoreline, representing 4.3 km of a total rocky shoreline of 52 km long. Therefore, less than 9% of this coast displayed suitable nursery grounds for *Diplodus* spp.

Quantification of *Diplodus* spp. settlers

At the scale of each of the three Calanques, maximum densities of settled *Diplodus* observed in each replicate nursery during the four-month monitoring period displayed high local variability, except in E4 (see coefficient of variation (CV) in Table 1). Therefore, no significant differences in mean maximum densities of *D. puntazzo* (Kruskal-Wallis, H=1.72; *P*=0.633) or *D. vulgaris* (Kruskal-Wallis, H=1.15; *P*=0.764) were found between Calanques.

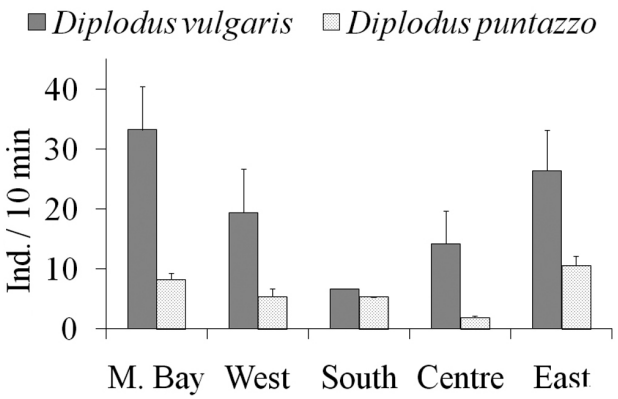

FIG. 3. – Mean density of *Diplodus* settlers (ind./10 min census) for each zone and species; error bars: standard error (SE).

At the regional-large scale, settler density significantly differed between zones for *D. puntazzo* (Kruskal-Wallis, H=12.08; *P*=0.016) (Fig. 3). *D. puntazzo* density was significantly higher in the east zone than in the centre zone (*P*=0.0067) and higher in Marseilles Bay than in the centre zone (*P*=0.0313). *D. vulgaris* densities showed a similar pattern but differences between zones were not significant (Kruskal-Wallis, H=4.99; *P*=0.288) due to high variability in the data from each zone (Table 2). For both species, the density observed was lowest in the south zone (the Riou archipelago), but this result relied on a single suitable site for settlement.

Microhabitat characteristics, settler behavior and temporal partitioning

The nursery characteristics of *Diplodus* settlers consisted in sheltered areas, characterized by shallow gently sloping bottoms composed of gravel, pebbles, or small boulders. High hydrodynamic conditions, abrupt slopes or the presence of vertical walls were unfavorable. Settlers were never observed on exclusively sandy bottoms or exclusively flat rocky flagstone. In the depth range surveyed (0-3 m) we noticed that *D. vulgaris* settlers were often dwelling deeper than *D.*

TABLE 2. – *Diplodus vulgaris* and *D. puntazzo* settler densities in the 23 large scale study sites along the rocky shore. Number of 10 minute counts per site (n), settler density per 10 minutes (density/10 min).

Zone	Site	n	*D. vulgaris* density/10 min	*D. puntazzo* density/10 min
Bay	B1	1	36.0	9.0
Bay	B2	3	16.7	5.3
Bay	B3	4	51.5	8.8
Bay	B4	7	28.6	10.1
West	W1	4	0.0	0.0
West	W2	7	5.1	2.9
West	W3	3	29.0	6.7
West	W4	3	24.0	6.7
South	S1	3	0.0	0.0
South	S2	3	0.0	0.0
South	S3	3	6.7	5.3
South	S4	3	0.0	0.0
Centre	C1	4	3.8	1.5
Centre	C2	3	22.7	2.7
Centre	C3	2	6.0	1.5
Centre	C4	4	24.5	1.8
East	E1	3	36.0	9.0
East	E2	3	0.0	0.0
East	E3	3	0.0	0.0
East	E4	3	22.7	11.7
East	E5	4	38.0	7.5
East	E6	3	9.0	14.3
East	E7	3	0.0	0.0

puntazzo settlers, which were restricted to the very shallow areas. This was particularly obvious during days with higher hydrodynamic conditions, when *D. vulgaris* took refuge in deeper water while *D. puntazzo* stayed in the surf zone.

An ontogenetic evolution of microhabitat use was observed: newly settled individuals showed high fidelity to these microhabitat preferences, subsequently their home-range became larger over time and older juveniles displayed a wider range of microhabitat use. In May-June, older *D. puntazzo* juveniles (i.e. recruits) were even observed dwelling out of their nursery habitats, over deeper and different microhabitats, which we interpreted as them starting to leave the nursery habitats to actively join adults (i.e. recruitment phase).

The abundance of *D. vulgaris* settlers was higher than that of *D. puntazzo*, both at local (3 Calanques pooled) ($U=6.16$; $P=0.013$) and regional scales: in the Marseilles Bay and centre zone the relative abundance of *D. vulgaris* settlers was significantly higher than that of *D. puntazzo* (respectively $H=5.33$; $P=0.02$ and $H=5.40$ and $P=0.02$).

In February 2004, *D. puntazzo* settlers observed in nurseries, according to their size (25-35 mm), settled there a few months earlier. In the same month, settlers of *D. vulgaris* were smaller in size (15-20 mm TL). These data indicate that in 2004 *D. vulgaris* settlement occurred from mid-February to early March. Although this study was restricted to *Diplodus puntazzo* and *D. vulgaris*, it is worth mentioning that in Endoume cove (Fig. 1), early settlers (about 20 mm TL) of *Diplodus sargus* (Linnaeus, 1758) were observed in June 2004 in the same nursery microhabitat.

DISCUSSION

Microhabitat characteristics, behavior of settlers and temporal partitioning

Our observations of microhabitat characteristics where settlement was observed confirmed the previously described requirements of *Diplodus* spp. for benthic settlement in terms of the biotic and abiotic characteristics of their nursery grounds (Harmelin-Vivien *et al*., 1995): sheltered areas with shallow gently sloping bottoms composed of gravel, pebbles, or small boulders without vertical walls and overhangs.

Our observations of *D. puntazzo* settlers were consistent with results from previous studies that indicate October-November as a settlement period for this species (García-Rubies and Macpherson, 1995; Macpherson, 1998; Vigliola, 1998). Vigliola (1998) observed settlement of *D. vulgaris* between October and March in 1994 and 1996, with a settlement peak between mid-December and mid-January. It therefore seems that *D. vulgaris* settlement was delayed in 2004. Our observation of early settlers of *D. sargus* in June was in agreement with previous studies which highlighted that the same nursery grounds are successively used by different *Diplodus* species, demonstrating a temporal partitioning of habitat use (García-Rubies and Macpherson, 1995; Harmelin-Vivien *et al*., 1995; Macpherson, 1998; Vigliola, 1998).

Thus, the studied microhabitats, given their intrinsic value as key nursery habitats within fish life cycles and their successive use over time by several species, appear to be particularly important for *Diplodus* stock renewal.

Quantification of nursery areas and settlement rates: a local and large-scale assessment

Mapping of microhabitats highlighted that suitable nursery grounds represented a low proportion of the rocky shore (9%) near Marseilles. Moreover, when present in a given Calanque (i.e. cove), nursery areas were found in the most vulnerable location: the innermost part of the cove, where human activities can cumulate and threat coastal habitat conservation, e.g. with direct impacts such as the destruction of microhabitats due to land being claimed from the sea (Meinesz *et al*., 2006). Consequently, human activities can affect *Diplodus* nursery grounds and settlement and thus the entire species life cycle through the replenishment of adult assemblages. These important biological areas for the *Diplodus* species are often targeted by coastal development programs, and therefore this issue is of special concern.

For a given year, settler density can be used as an indicator of the settlement rate in a given area. The settlement rate of *Diplodus* was highly variable at both scales studied: within Calanques (local scale) and between zones (regional scale). At the largest scale (amongst

zones), the lower densities observed in 2004 in the south and centre zones, compared to those recorded in the east and Marseilles Bay zones (ratio 1 to 4), suggest that repeated observations are necessary in the future to verify whether this was a sporadic phenomenon or if a recurrent settlement deficit might occur in these zones. A settlement deficit was also observed in Hyères Bay and Port-Cros National Park (70 km apart eastward, Var shoreline, France, NW Mediterranean Sea), where *Diplodus* densities accounted respectively for only 30 to 5% of those observed in Marseilles Bay in the same year (Harmelin and Vigliola, 1998).

At the local scale (within a Calanque), such as in Callelongue (site W4) and to a lesser extent in Sormiou (E1), the high variability of the maximum settler densities, reflected in the CVs, suggests that settlement processes could depend on local environmental conditions, such as subtle differences in microhabitat complexity and temperature, which influence settler growth rate and mortality through predation (stage-duration hypothesis) as demonstrated by Vigliola (1998). In contrast, the lower variability of maximum settler density observed in Morgiou (E4) suggests that more homogenous environmental conditions shape its nurseries. The geomorphology of each Calanque (Fig. 2) may also determine the patterns observed, even if currently the main factors driving this variability remain unknown, and need further investigation.

On the large scale, the absence of significant difference in *D. vulgaris* density between zones may have been due to high density variability at the local scale within each zone. The occurrence of several successive settlement events, inducing local density variability, could mask large scale patterns. This hypothesis was supported by field observations which revealed successive cohorts of *D. vulgaris* settlers in at least one site (Cheminée, unpublished data).

Harmelin and Vigliola (1998) concluded that the settlement deficit observed in Port-Cros National Park was probably due to oceanographic currents that might have exported reproduction products (eggs and larvae) far away from breeding areas. Based on the results of the present study, we may hypothesize that the settlement patterns observed could also have been influenced by local geomorphology and currents.

Harmelin-Vivien *et al*. (1995) observed a recruitment deficit in the Riou archipelago (south zone) for five Sparidae species, including *D. puntazzo* and *D. vulgaris.* Moreover, the size structure of adult *Diplodus* assemblages around Riou archipelago shows a deficit of the smallest size class compared to the Marseilles Bay assemblages. In our study, fewer settlers of *D. puntazzo* were observed in the Riou archipelago in comparison with Marseilles Bay and the east zone. These results supported the idea of a recurrent *Diplodus* settlement deficit in the Riou archipelago. In order to confirm the hypothesis of a settlement deficit in the centre zone, it would be interesting to study the adult assemblage size structure further.

In conclusion, our large-scale assessment of the nurseries of the Marseilles rocky shore led us to reject our null hypothesis: nurseries were not common along the rocky shore and did not display homogenous abundances of settlers. This study (i) allowed us to localize *Diplodus* nursery grounds precisely within three main Calanques, (ii) quantified and highlighted the scarcity (9%) and vulnerability of these nurseries along the entire rocky shore (low microhabitat availability), and (iii) gave an estimation of the settlement rates for 2004, suggesting a possible chronic settlement deficit in some zones (low settler supply). As a consequence, local nurseries alone might not be sufficient to replenish the adult assemblages of this shore, which may rely partly on the migration of adults or sub-adults first settling in other distant, more suitable areas, like the Marseilles Bay. Such a replenishment scenario has already been suggested by Harmelin-Vivien *et al*. (1995) and is similar to the one described for Port-Cros National Park by Harmelin and Vigliola (1998).

Coastal management implications

Nursery microhabitats are intrinsically important for species conservation and even more specifically for *Diplodus* because the same nursery grounds are successively used by different *Diplodus* species. In order to manage and protect *Diplodus* adult fish stocks along the rocky shore of Marseilles, our data (vulnerability of scarce local nurseries to coastal development) strongly indicate the need for protecting these nurseries. Nursery localizations should be taken into account for further integrated coastal management. Furthermore, since their scarcity may impair a full replenishment of adult assemblages, local coastal management needs to reinforce management in other nearby areas in order to allow distant nurseries to contribute to the renewal of the *Diplodus* adult assemblages along this rocky shore by supplying sub-adult migrants. In conclusion, all adult assemblages should have sufficient protected nursery grounds close enough to contribute to their replenishment (taking into account all relevant factors e.g. currents and distances). Reciprocally, when projects aimed at enhancing adult assemblages are devised (marine reserve, artificial reefs) they should be set next to or include nursery habitats in order to take advantage of the local adult reproductive potential (Francour *et al.*, 2001).

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REFERENCES

Ballesteros, E. – 2009. Is climate change the main driver of current community and landscape changes in the Mediterranean Sea? Oral communication. ASLO Aquatic Sciences Meeting 2009, 25-30 January 2009, Center of Congres Acropolis, Nice, France.

Brothers, E.B. and W.N. McFarland. – 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon fiavolineatum* (Desmaret), Haemulidae). *Rapp. P.-v. Reun. Cons. int. Explor. Mer*, 178: 369-374.

Chapman, M.G. – 1995. Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. *Mar. Ecol. Prog. Ser.*, 126: 191-202.

Francour, P., J.G. Harmelin, D. Pollard and S. Sartoretto. – 2001. A review of marine protected areas in the northwestern Mediterranean region: sitting, usage, zonation and management. *Aquatic Conserv. Mar. Freshw. Ecosyst.*, 11: 155-188.

Francour, P. and L. Le Direac'h. – 1994. Recrutement de l'ichtyofaune dans l'herbier superficiel à *Posidonia oceanica* de la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale) : données préliminaires. *Trav. sci. Parc. nat. reg. Corse,* 46: 71-91.

García-Rubies, A. and E. Macpherson. – 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. *Mar. Biol.*, 124: 35-42.

Guidetti, P. and S. Bussotti. – 1997. Recruitment of *Diplodus annularis* and *Spondyliosoma cantharus* (Sparidae) in shallow seagrass beds along the Italian coasts (Mediterranean Sea). *Mar. Life*, 7: 47-52.

Harmelin-Vivien, M. L., J.G. Harmelin, C. Chauvet, C. Duval, R. Galzin, P. Lejeune, G. Barnabé, F. Blanc, R. Chevalier, J. Duclerc and G. Lasserre. – 1985. Évaluation visuelle des peuplements et populations de Poissons : méthodes et problèmes. *Rev. Ecol. (Terre Vie),* 40: 467-539.

Harmelin-Vivien, M.L., J.G. Harmelin, and V. Leboulleux. – 1995. Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia*, 301: 309-320.

Harmelin, J.G. and L. Vigliola. – 1998. Renouvellement des populations de sars (*Diplodus spp.*) du parc national de Port-Cros : évaluation du potentiel. *Rap. Tech. Parc National Port-Cros, Programme Rech. 1996-97, 96.028.83400 PC.*

Le Direac'h, L. and P. Francour. – 1998. Recrutement de *Diplodus annularis* (Sparidae) dans les herbiers de posidonie de la Réserve Naturelle de Scandola (Corse). *Trav. sci. Parc. nat. reg. Corse,* 57: 42-75.

Levin, P.S. – 1994. Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. *Oecologia*, 97: 124-133.

Macpherson, E. – 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *J. Exp. Mar. Biol. Ecol.*, 220: 127-150.

Macpherson, E. and N. Raventos. – 2005. Settlement patterns and post-settlement survival in two Mediterranean littoral fishes: influences of early-life traits and environmental variables. *Mar. Biol.*, 148: 167-177.

Macpherson, E. and U. Zika. – 1999. Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean. *Mar. Ecol. Prog. Ser.*, 182: 269-282.

Meinesz, A., F. Javel, S. Longepierre, Vaugelas, J. de and D. Garcia. – 2006. Inventaire et impact des aménagements gagnés sur le domaine marin - côtes méditerranéennes françaises. *Univ. Nice-Sophia Antipolis, Lab. Ecomers: www.medam.org*.

Planes, S., E. Macpherson, F. Biagi, A. Garcia-Rubies, J.G. Harmelin, M. Harmelin-Vivien, J.Y. Jouvenel, L. Tunesi, L. Vigliola and R. Galzin. – 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. *J. Mar. Biol. Ass. U. K.*, 79: 137-143.

Raventos, N. and E. Macpherson. – 2005a. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. *Mar. Ecol. Prog. Ser.*, 285: 205-211.

Raventos, N. and E. Macpherson. – 2005b. Environmental influences on temporal patterns of settlement in two littoral labrid fishes in the Mediterranean Sea. *Est. Coast. Shelf Sci.*, 63: 479-487.

Sano, M. – 1997. Temporal variation in density dependence: Recruitment and postrecruitment demography of a temperate zone sand goby. *J. Exp. Mar. Biol. Ecol.*, 214: 67-84.

Vigliola, L. – 1998. *Contrôle et régulation du recrutement des Sparidés (Poissons, Téléostéens) en Méditerranée : importance des processus pré- et post-installation benthique.* Ph.D. thesis, Univ. Aix-Marseille II.

Vigliola, L., M. Harmelin-Vivien, F. Biagi, R. Galzin, A. García-Rubies, J.G. Harmelin, J. Y. Jouvenel, L. Le Direac'h-Boursier, E. Macpherson and L. Tunesi. – 1998. Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean. *Mar. Ecol. Prog. Ser.*, 168: 45-56.

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2.3 Paper: Fishery reserve effects on sparid recruitment along French Mediterranean coasts

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Fishery reserve effects on sparid recruitment along French Mediterranean coasts

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Abstract. Many studies have reported increasing trends in fish abundance and biomass inside marine reserves. This "reserve effect" may lead to increased fecundity and production inside the reserve, enhancing recruitment in surrounding areas. However, the increase in piscivorous and other large carnivorous fish species (i.e. predators) could also translate to higher predation inside the reserve, thus reducing recruitment. In this study, juvenile *Diplodus sargus* (Sparidae) were surveyed in their nursery habitats in Saint-Raphäel, French Mediterranean to determine the effects of protection on density and mortality. Visual census was undertaken weekly during the recruitment season (June to August 2011) in 12 nursery coves situated across two zones: inside the *Cantonnement de Pêche du Cap Roux* (Cap Roux Fishery Reserve) and outside (control) the reserve. There were no significant differences in juvenile peak density between zones although it was slightly higher outside than inside the reserve. Instantaneous mortality rate was significantly higher in the reserve than outside (1-way ANOVA, $p = 0.024$). Mortality seems to be density-independent. This study shows indications that recruitment of the rocky reef fish, *D. sargus*, is lower inside the reserve compared to nearby fished areas and that this pattern could be attributed to predation. However, further research is warranted to obtain more unequivocal conclusions.

Key words: Recruitment, Mortality, Fishery reserve, Sparidae, Mediterranean.

Introduction

Various studies have documented the positive effects of protection on fish assemblages, especially commercially-exploited species. Higher fish abundance and biomass have been observed inside marine reserves than in unprotected areas (e.g. Polunin and Roberts 1993; Claudet et al. 2008; Molloy et al. 2009). Marine reserves have been promoted as a management strategy to improve and sustain adjacent fisheries (e.g. Roberts and Polunin 1991; Seytre and Francour 2008) possibly either through the net emigration of adults and juveniles across boundaries (i.e. spillover) and/or the export of pelagic eggs and larvae which is enhanced by the increased production and fecundity inside the reserve (Rowley 1994; Russ 2002; Garcia-Charton et al. 2008). Despite the growing literature on the biological and ecological effects of protection on fish populations, its effect on recruitment has been infrequently studied (Pelletier et al. 2005).

Recruitment, as used in this study, refers to the number of post-transition juveniles (already adapted to necto-benthic life) and immature adults (already attained adult-like morphology and coloration), as defined by Vigliola and Harmelin-Vivien (2001). It differs from settlement, which is the process of moving from the pelagic zone to the benthic habitat (Sale et al. 1984). The maximum density of settlers ("peak density") best accounts for the settlement event intensity ("settlement rate"), i.e. the number of new individuals joining the benthic habitat for a given nursery area. The number of juveniles remaining at the end of the post-settlement period, (i.e. settlers who survived arbitrary periods of time after settlement and may join adult assemblages), gives a proxy of the recruitment success for a given nursery habitat (Levin 1994a, 1994b; Macpherson 1998). This recruitment success ("recruitment level") can be assessed by monitoring the mortality of juveniles during the post-settlement period in the nursery until their dispersal towards adult habitats (Macpherson et al. 1997).

Protection can have two possible opposing effects on recruitment inside marine reserves: (1) enhancement, due to the protection of preferred habitats and lower disturbance which is especially relevant to settling larvae with distinct habitat preferences (Planes et al. 2000) and to increased abundance of adult conspecifics (Arceo et al. 2007); or (2) reduction, due to higher mortality caused by increased predation (Tupper and Juanes 1999; Webster 2002). The present study focuses on the second hypothesis. Early juvenile survivorship is potentially important in determining recruitment rate variation to older age classes if post-settlement mortality is high (Sale and Ferrel 1988) and if recruitment is low (Fontes et al. 2009). Because of the increase in piscivorous and other large carnivorous fish species (i.e. predators) inside marine reserves as observed in previous studies, juvenile fish mortality could be higher, resulting to lower levels of recruitment. Macpherson et al.

(1997) have previously reported no significant differences in juvenile fish mortality between protected and unprotected areas in the northwestern Mediterranean. However, their study pooled sites across a large geographic scale (i.e. three countries), and may have masked the intrinsic characteristics of the protected areas surveyed.

The objective of this study was to determine the effects of protection on juvenile fish density (settlement intensity) and mortality (proxy of recruitment success) at a local scale. More specifically, abundances of juvenile sea breams, *Diplodus sargus* (Sparidae), were monitored in their natural nursery habitats in and around a fishery reserve in Saint-Raphäel, French Mediterranean during the 2011 recruitment season. *D. sargus* was selected as the focal species because of its well-described seasonality and habitat requirements during settlement (Garcia-Rubies and Macpherson 1995; Harmelin-Vivien et al. 1995; Macpherson 1998; Vigliola and Harmelin-Vivien 2001; Cheminée et al. 2011). Furthermore, it is a commercially-targeted species for both recreational and professional fisheries. Mortality rate of juvenile *D. sargus* inside and outside the reserve was then computed. Indicative patterns of mortality are presented, and their implications to marine reserve dynamics are briefly discussed.

Material and Methods

Study Area

The study was conducted in the *Cantonnement de Pêche du Cap Roux* (Cap Roux Fishery Reserve) and adjacent areas in Saint-Raphaël, along the French Mediterranean coast (Fig. 1). The fishery reserve was established in December 2003 through the initiatives of the professional fishers from the *Prud'homie de Pêche* of Saint Raphaël. The reserve is a no-take zone, and covers an area of approximately 450 hectares extending from the coastline up to the 80-meter isobath.

An initial survey was conducted in December 2009 to identify suitable nursery habitats for *D. sargus* in and adjacent to the Cap Roux Fishery Reserve. This species settles onto very shallow waters (0-1 m), usually within small coves that are rocky on both sides of the beach and with a gently sloping heterogeneous substrate consisting of coarse sand, pebbles and boulders (Harmelin-Vivien et al. 1995). Based on these characteristics, twelve coves (sampling stations) were then selected: four to the north, four inside and four to the south of the reserve (Fig. 1). Care was taken in the cove selection such that they were similar in substrate characteristics and that they were sufficiently separated from neighboring coves to avoid movement of juvenile fish among coves which could bias estimation of mortality rates. Juveniles of *D. sargus* display high fidelity to their nursery habitat and start to move to deeper waters only around 6 months after settlement at 50-60 mm lengths (Garcia-Rubies and Macpherson 1995).

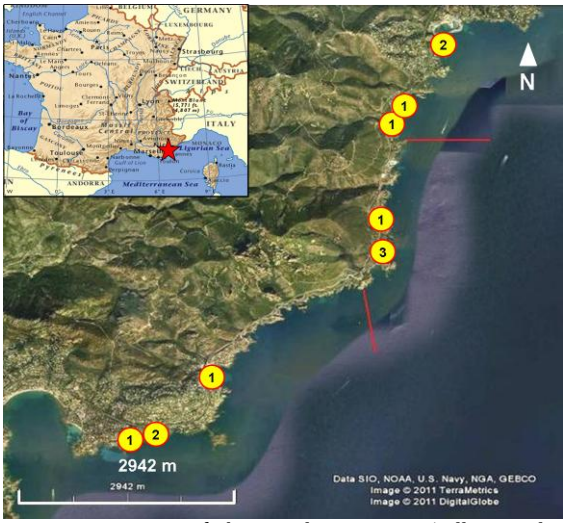

Figure 1: Location of the sampling stations (yellow circles indicating the number of coves) inside and adjacent to the Cap Roux Fishery Reserve and its boundaries (red line). (Map source: Google-Earth). Inset map: France.

Field Methods

An initial study done during the recruitment season in 2010 validated the presence of settlers in the selected sampling stations. However, only 2 surveys could be done (June and August) and data were excluded from the analyses. For the main experiment, surveys were done weekly, weather permitting, from 14 June to 17 August 2011. This resulted to seven separate surveys over 10 weeks.

To count the juvenile fish in the sampling stations, the methods described in Cheminée et al. (2011) were followed. The abundance and size of all juvenile *D. sargus* encountered were estimated using underwater visual census wherein an observer snorkeled very slowly along the shoreline of the entire cove, covering a narrow strip from the shore up to 10 meters seawards (variable depending on the physical characteristic of each cove) with a depth range of 0-2 m. Hence, the whole nursery area is usually covered. The slow swimming avoids disturbing the juveniles and allows for ease in counting and size estimation (Harmelin-Vivien et al. 1985). Total length was estimated using a diagram of fish silhouettes of 5-mm size classes as a guide. The precision of this method is approximately ±3.5 mm for *Diplodus* species (Macpherson 1998). Data were recorded on a plastic slate. Surveys were done around the same time of the day (0900 – 1500) and completed for all coves in two days. Other observations, such as water turbidity and weather conditions, were also noted.

Data Analysis

Mean peak density (abundance over the total area surveyed for each cove and standardized to 100 m^2) of juvenile *D. sargus* was obtained and compared

between the two zones (reserve and control). Data for the north and south stations were pooled into the control zone since the means were very similar in terms of values; hence, an unbalanced design having 4 replicates for the reserve and 8 replicates for the control was used in the analyses.

To estimate mortality, individual abundance values for each survey were log-transformed (ln x+1) and plotted over time (in days) starting from the time of peak abundance for each cove. The resulting slope of this linear regression corresponds to the instantaneous mortality rate. The use of time-series data has been suggested to be more accurate in estimating mortality rates compared to using only the final and initial density values (see Macpherson et al. 1997).

One-way Analysis of Variance (ANOVA) was then used to test for differences in juvenile density and mortality rate between the two zones. Cochran's test was used to test for homogeneity of variances. The effect size Hedges' *g* (which takes into account unequal sample sizes) and statistical power were also computed using packages in the R Software (version 2.15.0).

The correlation between peak density and mortality rate was determined using Spearman's Rank Correlation Coefficient.

Results

Settlement of *D. sargus* in the sampling stations occurred in a single pulse with all but two stations showing peak abundances during the second survey (5 to 8 days after the first survey). The sizes of the juvenile fish recorded ranged from >10 mm to 60 mm. The smallest size classes (>10 to 25 mm) were observed during the first 3 surveys, and the dominant size class on the last survey ranged from 40-55 mm.

Mean peak densities (*standard deviation*) in the reserve and control stations were 5.65 (*2.11*) and 7.83 (*3.71*) individuals per 100 m^2, respectively. There were no statistically significant differences between zones [F(1,10) = 1.154, p = 0.308] although peak density was slightly lower in the reserve than in the control (Fig. 2). The effect size for this difference (*g* = 0.6072), when converted to Cohen's (1988) convention for *d*, is moderate. Post-hoc analysis showed the power of the test to be low

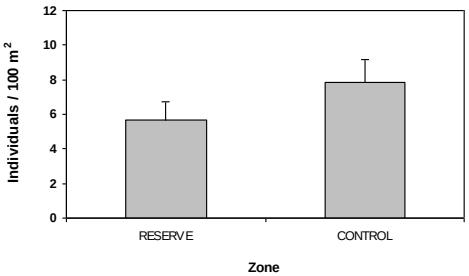

Figure 2: Mean peak density (± SE) of juvenile *Diplodus sargus* inside (reserve) and outside (control) the Cap Roux Fishery Reserve.

(0.164). Increasing the power to the recommended 0.80 level to detect the same moderate effect would require a sample size of 38 for each zone.

The highest reduction in abundance of juveniles was mainly observed between the second (observed peak abundance) and third surveys which were 6 to 8 days apart. In 10 out of the 12 sampling stations, at least 50% up to 80% of the newly-settled juveniles (size class of >10 to 15 mm) were lost during this period. There was a statistically significant difference in mean instantaneously mortality rate between zones [F(1,10) = 7.076, p = 0.024], with mortality rate being higher inside the reserve than in the control (Fig. 3). The effect size was high (g = 1.504) and the power was approximately 0.670. A balanced design of 8 replicates per zone would have further increased the power to the recommended 0.80 level.

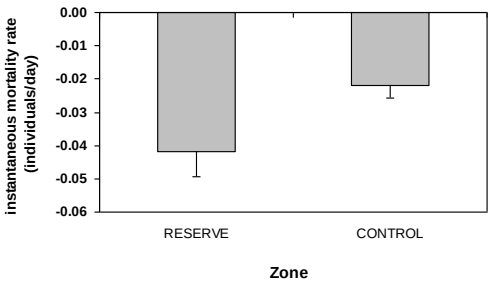

Figure 3: Mean instantaneous mortality rate (± SE) of juvenile *Diplodus sargus* inside (reserve) and outside (control) the Cap Roux Fishery Reserve.

A comparison between mortality rate and peak density indicated no significant pattern (Table 1). The correlation between the two variables showed a non-significant relationship (Spearman R = -0.014, p = 0.965).

Zone	Station	Mortality	Density *(Peak / Final)*
Reserve	Maubois	-0.05927	5.75 / 0.05
	Nbeach 1	-0.02936	6.74 / 1.63
	Nbeach 2	-0.02905	7.45 / 2.24
	Nbeach 3	-0.04985	2.66 / 0.16
Control (north)	Figuer 1	-0.00831	4.46 / 1.34
	Figuer 2	-0.02745	1.67 / 0.42
	Trayas 2	-0.02046	11.20 / 2.36
	Trayas 3	-0.03687	13.10 / 1.81
Control (south)	Antheor 1	-0.01662	6.41 / 2.43
	Anglais 1	-0.02792	7.98 / 1.21
	Anglais 2	-0.03119	10.28 / 2.38
	Anglais 3	-0.00777	7.57 / 2.86

Table 1: Mean mortality rate (individuals per day) and density (peak and final, in individuals per 100 m^2) of juvenile *D. sargus* across the sampling stations in the two zones.

Discussion

Several factors have been observed to influence the survival of juvenile fish after settlement: abiotic sources of mortality (i.e. disturbance), predation (e.g. encounter rates, vulnerability), competitive interactions with residents (conspecifics, juvenile/adults, predators) and availability of resources such as food or shelter (Shulman 1985; Piko and Szedlmayer 2007; Juanes 2007). In MPAs, predation on juvenile fish can be higher due to an increased number of piscivorous fish usually targeted by fishing (Tupper and Juanes 1999). This increased predation has been observed for juveniles of a commercially important invertebrate, the spiny lobster *Palinurus elephas*, inside the Medes Islands MPA in the northwestern Mediterranean (Diaz et al. 2005). The higher predator biomass inside MPAs, as has been observed in some Mediterranean MPAs (Francour et al. 2010), could mean more intense predation so that local survivorship could be affected. The present study was able to detect significantly higher mortality patterns of juvenile *D. sargus* inside the reserve compared to the outside areas (at $p<0.05$). These results differed with Macpherson et al. (1997) who did not find significant differences in juvenile mortality for the same species between inside and outside MPAs. The potential predators of *D. sargus* juveniles are mainly small predatory species or small individuals of large species that may not be seriously affected by the reserve effect (Macpherson et al. 1997). However, in the shallow *Posidonia oceanica* meadows of the Cap Roux Fishery Reserve, Seytre and Francour (2009) highlighted significant differences between the density of Serranidae inside and outside the reserve (Reserve > Outside). In all the 12 sampled coves of the present study, the bottom is covered by dense *P. oceanica* meadows, ending some meters before the beaches. Seagrass habitats are therefore close to the nursery habitats so that Serranidae could represent potential predators of the sparid juveniles that respond to protection. Continued recruitment surveys will be needed to take into account the natural spatial and temporal variability of recruitment and obtain more conclusive results.

Most species experience the greatest rates of mortality during their early weeks in the coral reef environment (e.g. Victor 1986, Schmitt and Holbrook 1999; Almany and Webster 2006, Holmes and McCormick 2006) although this may widely vary among species (Steele and Forrester 2002). Similar patterns have been observed for temperate species. For example, Planes et al. (1998) report that 24.3% to 99.4% of the initial population of *Diplodus* spp. disappeared within three months after settlement. The results of the present study were consistent with these observations. A reduction of 50-80% of the smallest size class (i.e. recently-settled) occurred approximately one week after settlement.

The lack of correlation between mortality and peak density suggests that mortality of juvenile *D. sargus* in the study area is not density-dependent. In fact, the reserve zone had slightly lower peak density but higher mortality rate than the outside zones. Previous studies have also reported density-independent juvenile mortality in some coral reef (e.g. Victor 1986, Jones 1987) and temperate (Levin 1994a) fish species. In opposition to these findings, Macpherson et al. (1997) and Planes et al. (1998) observed strong density-dependent mortality rates for juveniles of *Diplodus* spp. However, when mortality rates of *D. sargus* were compared in protected and unprotected sites in the northwestern Mediterranean, there were no significant differences among sites (Planes et al. 2000). Whether increased predation on juvenile fish in protected areas, when present, is a major factor influencing natural recruitment patterns cannot be ascertained in the present study. White (2007) has observed a strong relationship between predator abundance and the nature of density-dependent mortality of *Thalassoma bifasciatum* settlers. He noted that wrasse mortality was inversely density-dependent in sites with few predators and positively density-dependent in sites with higher predator densities. Hixon and Carr (1997) also observed that mortality of juvenile *Chromis cyanea* is spatially density-dependent in the presence of two suites of predators (transients and residents) but density-independent in the absence of these predators.

The present work is one of few studies specifically designed to test the effects of protection on fish recruitment. It has shown indicative results that recruitment of the rocky reef fish, *Diplodus sargus*, is lower inside a reserve compared to fished areas and that this pattern could be attributed to predation. This observation suggests that protection may have a more substantial effect on fish recruitment, specifically on post-settlement mortality, as previously observed. Due to the possible variation of recruitment between years and lag time of ecological responses to protection, censuses have to be continued for several years to monitor juvenile densities and mortality and obtain unequivocal results. The geographic scale of the experimental design, i.e. proper controls or outside sampling stations near the MPA being studied, should also be carefully considered because it could influence the sensitivity of the study to detect protection effects on fish recruitment.

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References

Almany GR, Webster MS (2006) The predation gauntlet: early-post-settlement mortality in reef fishes. Coral Reefs 25:19-22

Arceo HO, Aliño PM, Nañola CL (2007) Adult-juvenile reef-fish relationships and their significance to marine protected areas. In Day JC, Senior J, Monk S, Neal W (eds) First Intl Mar Protected Areas Congress, 23-27 October 2005, Conference Proc, Geelong, Victoria, Australia, 1:358-360

Champely S (2009) pwr: Basic functions for power analysis. R package version 1.1.1. http://CRAN.R-project.org/package=pwr

Cheminée A, Francour P, Harmelin-Vivien M (2011) Assessment of Diplodus spp. (Sparidae) nursery grounds along the rocky shore of Marseille (France, NW Mediterranean). Sci Mar 75:181-188

Claudet J, Osenberg CW, Benedetti-Cecchi L, Domenici P, Garcıa-Charton JA, Perez-Ruzafa A, Badalamenti F, Bayle-Sempere J, Brito A, Bulleri F, Culioli J, Dimech M, Falcon JM, Guala I, Milazzo M, Sanchez-Meca J, Somerfield PJ, Stobart B, Vandeperre F, Valle C, Planes S (2008) Marine reserves: size and age do matter. Ecol Letters 11:481-489

Cohen J (1988) Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Inc., New Jersey

Del Re AC (2012). compute.es: Compute Effect Sizes. R package version 0.2.1. http://CRAN.R-project.org/package=compute.es

Diaz D, Zabala M, Linares C, Hereu B, Abello P (2005) Increased predation of juvenile European spiny lobster (*Palinurus elephas*) in a marine protected area. New Zeal J Mar Fresh 39:447-453

Fontes J, Caselle JE, Afonso P, Santos RS (2009) Multi-scale recruitment patterns and effects on local population size of a temperate reef fish. J Fish Biol 75:1271-1286

Francour P, Mangialajo L, Pastor J (2010) Mediterranean marine protected areas and non-indigenous fish spreading. in Galani D, Appelbaum-Galani B (eds.) Fish invasions of the Mediterranean Sea: change and renewal. Pensoft Publishers, Sofia-Moscow, pp 35-56

Garcıa-Charton JA, Perez-Ruzafa A, Marcos C, Claudet J, Badalamenti F, Benedetti-Cecchi L, Falcon JM, Milazzo M, Schembri PJ, Stobart B, Vandeperre F, Brito A, Chemello R, Dimech M, Domenici P, Guala I,, LeDireach L, E.Maggi E, Planes S (2008) Effectiveness of European Atlanto-Mediterranean MPAs: do they accomplish the expected effects on populations, communities and ecosystems? J Nature Cons 16:193-221

García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar Biol 124:35-42

Harmelin-Vivien ML, Harmelin JG, Leboulleux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. Hydrobiologia 300/301:309-320

Harmelin-Vivien M, Harmelin JG, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J, Lassère G (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. Rev Ecol (Terre Vie) 40 :467–539

Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946-949

Holmes TH, McCormick MI (2006) Location influences size-selective predation on newly settled reef fish. Mar Ecol Prog Ser 317:203-209

Jones GP (1987) Competitive interactions among adults and juveniles in coral reef fishes. Ecology 68:1534-1547

Juanes F (2007) Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. J Fish Biol 70: 661-677

Levin P (1994a) Fine scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97:124-133

Levin P (1994b) Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environ Biol Fish 40:271-281

Macpherson E (1998) Ontogenetic shifts in habitat and aggregation in juvenile sparid fishes. J Exptl Mar Biol Ecol 220:127-150

Macpherson E, Biagi F, Francour P, Garcia-Rubies A, Harmelin J, Harmelin-Vivien ML, Jouvenel JY, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus *Diplodus* in protected and unprotected areas in the western Mediterranean Sea. Mar Ecol Prog Ser 160:135-147

Molloy PP, McLean IB, Côté IM (2009) Effects of marine reserve age on fish populations: a global meta-analysis. J Appl Ecol 46:743-751

Pelletier D, Garcia-Charton JA, Ferraris J, David G, Thebaud O, Letourneur Y, Claudet J, Amand M, Kulbicki M, Galzin R (2005) Designing indicators for assessing the effects of marine protected areas on coral reef ecosystems: a multidisciplinary standpoint. Aquat Living Resour 18: 15-33

Piko, A.A., and Szedlmayer, S.T. (2007) Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper. J Fish Biol 70:758-769.

Planes S, Jouvenel JY, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. Oikos 83:293-300

Planes S, Galzin R, Garcia-Rubies A, Goni R, Harmelin JG, Le Direac'h L, Lenfant P, Quetglas A (2000). Effects of marine protected areas on recruitment processes with special reference to Mediterranean littoral ecosystems. Environ Conserv 27: 126-143

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral reef fishes in 2 small Caribbean marine reserves. Mar Ecol Prog Ser 100:167-176

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-70-0, http://www.R-project.org

Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? Rev Fish Biol Fisher 1:65-91

Rowley RJ (1994) Case studies and reviews – marine reserves in fishery management. Aquat Conserv 4: 233-254

Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. in Sale PF (ed) Coral reef fishes - dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, pp 421–443

Sale PF, Ferrel DJ (1988) Early survivorship of juvenile coral reef fishes. Coral Reefs 7:117-124

Sale P, Douglas WA, Doherty PJ (1984) Choice of microhabitats by coral reef fishes at settlement. Coral Reefs 3:91-99

Schmitt RJ and SJ Holbrook (1999) Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80:35-50

Seytre C, Francour P (2008) Is the Cap Roux marine protected area (Saint Raphaël, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. Aquat Living Res 21:297-305

Seytre C, Francour P (2009) The Cape Roux marine protected area (Saint-Raphaël, French Mediterranean Sea): changes in fish assemblages within four years of protection. ICES J Mar Sci 66:180-187

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66:1056-1066

Steele MA, Forrester GE (2002) Early postsettlement predation on three reef fishes: effects on spatial patterns of recruitment. Ecology 83:1076-1091

Tupper, M, Juanes F (1999) Effects of a marine reserve on recruitment of grunts (Pisces: Haemulidae) at Barbados, West Indies. Environ Biol Fish 55:53-63

Victor BC (1986) Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol Monogr 56:145-160

Vigliola L, Harmelin ML (2001) Post-settlement ontogeny in three Mediterranean reef fish species of the genus, Diplodus. Bull Mar Sci 68:271-286

Webster MS (2002) Role of predator in the early-settlement demography of coral-reef fishes. Oecologia 131: 52-60

White JW (2007) Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality

2.4 Chapter conclusion: paper results synthesis and discussion

-In both studied localities (Marseilles and Esterel coast), *Diplodus* nursery habitats represent a low proportion of the coastline: along Marseilles rocky shore, less than 9 % of the coast displayed nursery habitats for these species (see paper in 2.2). Along the Esterel coast (paper in 2.3), the preliminary micro-habitats survey performed in 2009 allowed us to localize and map all potential *Diplodus* nurseries present along this coast: the 12 studied coves in the paper amount for about half of the total amount of *Diplodus* nursery habitat, which we estimate it represents as well less than 10 % of this shoreline (authors' unpublished data). In both localities these habitats are located in the most vulnerable locations, i.e. in the inner most part of coves where human activities cumulate their impacts.

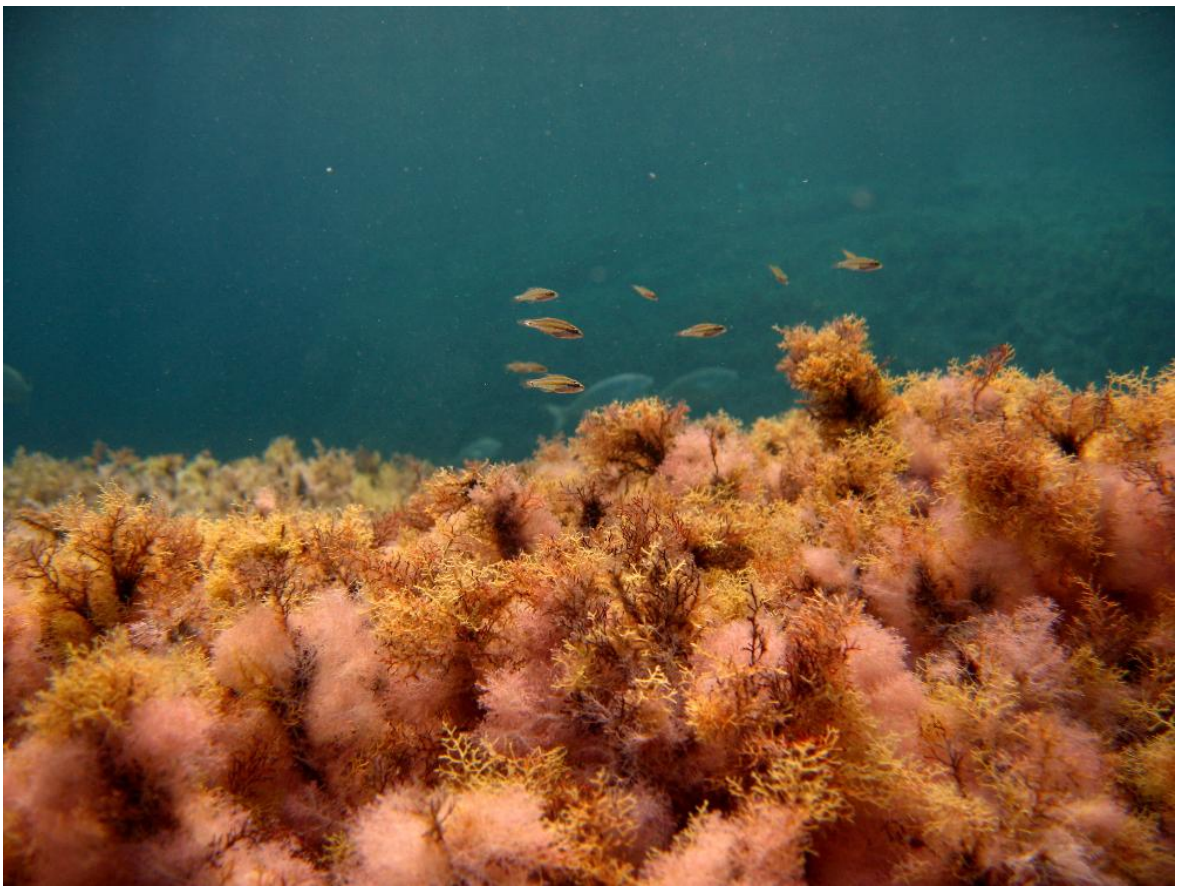
-Besides, in both localities, settlement rate (i.e. the maximum density of settlers reached for a given year in a given nursery) of the most abundant of the studied species (respectively *D. vulgaris* in Marseilles and *D. sargus* in Esterel) was highly variable in space at all spatial scales studied (from the cove scale to the entire locality scale).

-Within both MPAs (Calanques National Park and Cap Roux No-take zone), given the scarcity of nursery habitats and the spatial variability of settlement rates, our studies raise the following question: is the amount of existing nursery habitats (<10% of the shoreline) sufficient to replenish by itself local adult populations? Recruitment failure is possible in case of increased anthropogenic pressure on these essential habitats. Adult replenishment may thus rely on migration of adults or sub-adults previously settled in other nurseries, located outside the MPAs, i.e. for example respectively in the non-protected Marseilles Bay and la Napoule-Cannes Gulf. Such replenishment scenario has been hypothesized for other localities (Harmelin and Vigliola, 1998). This connectivity between every essential habitat of these species life cycle (spawning grounds, nursery grounds, others adult habitat), at each life-cycle stages (larval, juvenile, adult), requires to be assessed in each locality, as it was done for example along the South-western Adriatic coast (Di Franco et al., 2012). Such studies are ongoing in the NW Mediterranean, notably in the frame of European projects (e.g. WP 3.2 of MMMPA Training Network: "Connectivity of Mediterranean reef fish populations and MPA design", Garcia-Charton et al, Universidad de Murcia).

-No-take areas have been promoted to increase local fish assemblage biomass and favor biomass exportation towards fishing grounds (Polunin and Roberts, 1993; Roberts and Polunin, 1991; Seytre and Francour, 2008). However these reserve and spill-over effects still depend on the initial recruitment of individuals after their settlement in nurseries located within the MPA or immigration of young recruits from distant nurseries. Once the connectivity between essential habitats have been assessed, fish stock management

consequently relies on the protection of these essential habitats (including nurseries) both within no-take zone and outside no-take zone if not present or rare inside, as it is the case in the present studies. This raises a general question applicable in every coastal area: are essential habitats, notably nursery grounds, and their connectivity taken into account in the spatial design of management measures? In other words, are sufficient proportions of e.g. nursery habitats covered by existing protection levels in order to ensure protection of these key habitat functions and therefore guarantee coastal adult assemblage replenishment? These questions have been raised early in tropical areas since the 80's (Jones et al., 2009; McCook et al., 2009; Roberts, 1997; Sale, 2004; Turgeon et al., 2010). Chapter V addresses this issue in the context of Mediterranean Sea.

Chapter III. Nursery value of macrophyte-formed infralittoral habitats



Marina d'Elbu, Elbu bay, Scandola Natural Reserve, Corsica (-1.8 meters), 18th of September 2009 – Juveniles of *Symphodus ocellatus* (20-30 mm TL) dwelling above a *Cystoseira crinita* forest; when frightened they sought refuge below the canopy

Chapter III. Nursery value of macrophytes-formed infralittoral habitats

3.1 Chapter introduction

In the Chapter II, we studied along rocky shores the relative abundance and spatial distribution of nursery habitats for *Diplodus* spp., i.e. species for which nursery habitat characteristics have been described previoulsy (Bussotti and Guidetti, 2010; Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995). In order to manage coastal fish assemblages, managers need as well to know which other infralittoral habitats have a high nursery value –*sensu* Beck et al (2001)– for others littoral species and therefore deserve special management measures. Among the mosaic of the Infralittoral, photophilic macrophytes form habitats covering a large proportion of both soft and hard bottoms (Ballesteros, 1992; Clarisse, 1984; Pergent-Martini et al., 1994). Among them, *Posidonia oceanica* meadows are typically cited as nursery habitat for some species (e.g. *Diplodus annularis*, *Spondyliosoma cantharus*) (Guidetti, 2000). Furthermore, canopy forming macroalgal assemblages (i.e. erect Multicellular Photosynthetic Organisms belonging to the Chlorobionta, Rhodobionta and Phaeophyceae) may form wide forests covering infralittoral rocky biotope. It is notably the case of the arborescent *Cystoseira* species (Fucales, Chromobiontes, Straménopiles) (Fig. 1). Some rare studies suggested the nursery role of these forests (Riccato et al., 2009) but its nursery value – *sensu* Beck et al. (2001) – has never been assessed quantitatively and compared to alternate stable states –*sensu* Knowlton (2004) – such as Dictyotales-Sphacelariales bushland (Fig. 1). Likewise their spatial or temporal variability remains unknown and comparisons of the nursery value of Mediterranean macrophyte-formed habitats (e.g. *P. oceanica* meadows *vs Cystoseira* forests) are also lacking. Finally, underlying processes driving density patterns of juvenile fish densities across habitats were explored in other areas (Nanjo et al., 2011) but are still required in the Mediterranean.

Fig. 1. The main studied habitats: *Cystoseira crinita* forests, *Cystoseira balearica* forests, Dictyotales-Sphacelariales bushland

Therefore, this chapter aimed at answering these four questions. I used densities of juveniles as a proxy of nursery value –*sensu* Beck et al (2001)– but since density is only one of the four factors that must be considered to assess whether a habitat serves as a nursery (Beck et al., 2001), I also aimed at studying factors and their impacts that shape juvenile density patterns across habitats and within a given habitat, such as predation mortality and habitat tri-dimensional structure. This chapter is organized as follow: each part and sub-part is presented either as an article submitted for publication, in preparation, or as supplementary preliminary data:

- Part 3-2: "Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes" (submitted paper)
- Part 3-3: "Supplementary data: Spatial and temporal variability of fish juvenile densities within *Cystoseira* forest and Dictyotales - Sphacelariales bushland - preliminary results"
- Part 3-4: "Supplementary data: Comparison of fish juvenile densities within two canopy forming habitats, *Cystoseira* forests *vs Posidonia oceanica* meadows"
- Part 3-5: "Which may be the underlying processes explaining macrophytes-formed habitats nursery value?" (1 accepted paper, 1 paper in prep, some supplementary data)

3.2 Nursery value of Cystoseira forests for Mediterranean rocky reef fishes

Under review in Journal of Experimental Marine Biology and Ecology (submitted July 13, 2012); first referee conclusion: "accepted with minor revisions"; others referees conclusions coming soon.

In this paper, we present data of my first year of PhD (2009). During this first year I developed various methodologies in order to study juvenile fishes, both observational and manipulative, which are quite well detailed in the M&M section of this paper. Additional illustrations of field works can also be found in Chapter IV, where the same methodologies were employed.

Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes

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ABSTRACT

The canopy-forming fucoid *Cystoseira* spp. provide biogenic structure, food and shelter for many organisms including fishes on Mediterranean nearshore rocky reefs. Infralittoral *Cystoseira* forests have declined or disappeared from many Mediterranean locales, leading to a severe transformation of the habitat and the loss of its tri-dimensional structure. Here we assess the nursery value of *Cystoseira* forests and the consequences of this habitat transformation on the recruitment of rocky reef fish assemblages. Densities of several reef fish juveniles - particularly *Symphodus* spp. - were 9 to 12 folds greater in *Cystoseira* forests than in other erect and turf algal assemblages. Experimental habitat manipulation mimicking the alteration of a *Cystoseira* canopy showed greater abundances of *Symphodus* spp. juveniles on artificially forested substratum than on bare substratum. Our study quantified for the first time the nursery value and functional importance of *Cystoseira* forests canopies suggesting that their loss may strongly affect the recruitment of littoral fishes in the Mediterranean Sea.

KEYWORDS

Cystoseira, nursery value, canopy, alternate stable states, fish juveniles, *Symphodus*

1. Introduction

Rocky infralittoral habitats have been transformed dramatically in the last decades in the North-Western Mediterranean, due to several human-induced modifications (Milazzo et al., 2004a; Planes et al., 1999; Sala et al., 1998; Sala et al., 2011; Verlaque, 1994). Among recent habitat transformations, formerly abundant macroalgae forests (i.e. Multicellular Photosynthetic Organisms belonging to the Chlorobionta, Rhodobionta and Phaeophyceae) formed by the genus *Cystoseira* are virtually gone (Thibaut et al., 2005). Mostly due to anthropogenic disturbances, most *Cystoseira* species show severe regression if not local extinction (Hoffmann, 1988; Mangialajo et al., 2008; Mangialajo et al., 2007). Most of these canopy-forming species used to be dominant in Mediterranean rocky reefs (Clarisse, 1984), creating a complex tri-dimensional structure and harboring high biodiversity and productivity (Ballesteros, 1992; Ballesteros et al., 1998; Hoffmann et al., 1992; Terradas et al., 1989). These disturbances can lead to community shifts, whereby *Cystoseira* forests are replaced by alternate stable states (*sensu* Knowlton (2004) and references therein) without canopy and dominated by other erect macroalgae (e.g., Dictyotales and Sphacelariales), turf algae, or sea urchin barrens dominated by encrusting Corallinaceae (Bonaviri et al., 2011; Hereu, 2004). Very early in marine science history (Figuier, 1869) the canopies of submarine "forests" (e.g. kelps) have been mentioned as refuge and feeding habitat for fish. In other temperate or sub-tropical seas, the nursery role of canopies for juvenile fishes has been highlighted, such as for giant kelp (*Macrocystis* sp.) forests (Carr, 1989), for Serranidae (Carr, 1994) and Labridae (Jones, 1984) or *Sargassum* beds for *Mycteroperca rosacea* groupers (Aburto-Oropeza et al., 2007). In the NW Mediterranean, a strong association of adult labrids with rocky bottoms covered by dense erect macroalgae has been shown, either for foraging activities of adults (Bell and Harmelin-Vivien, 1983) or for the building of their nests (Lejeune, 1985). Along the Catalan coast of Spain, Garcia-Rubies and Macpherson (1995) showed that juveniles of two *Symphodus* (Labridae) species were mostly found on rocky substrate with dense cover of erect macroalgae. However, very few studies explored the role of *Cystoseira* forests themselves as nursery habitat for juvenile fish (Riccato et al., 2009) and none did quantify its "nursery value" i.e. "the production of individuals that recruit to adult populations per unit area of juvenile habitat" (Beck et al., 2001). Moreover previous studies in subtropical and temperate seas show that modification of macroalgal cover can affect the abundance, composition and survival of juvenile fishes (Aburto-Oropeza et al., 2007; Carr, 1989; Deza and Anderson, 2010; Levin and Hay, 1996; Macpherson and Zika, 1999) which in turn may lower habitat's nursery value and therefore compromise its "nursery role" (i.e. a habitat plays a "nursery role" for juveniles of a given specie if its nursery value is greater in average than in other habitats in which juveniles occur, *sensu* Beck et al. (2001)). In the Mediterranean, impacts of the modification of macrophyte assemblages on fish have been discussed in the frame of the invasion by the tropical alga *Caulerpa taxifolia* (Francour et al., 1995; Levi and Francour, 2004; Longepierre et al., 2005). Thibaut et al. (2005) suggested the

potential ecological consequences of the loss of the *Cystoseira* forests, since its complex tri-dimensional structure is a source of food and shelter for many species. However, the impacts of this habitat shift are largely unknown, although we can assume that any impacts to the juvenile stage of reef fishes will also affect adult fish populations, and consequently fisheries (Cheminée et al., 2011; Harmelin-Vivien et al., 1995).

This study aims at answering two main questions: (1) what is the nursery value of *Cystoseira* forests for juvenile fish? (2) What are the consequences of the depletion of *Cystoseira* forests? To answer these questions we conducted underwater visual census and experiments in two sites in Corsica and southern France.

2. Material and methods

2.1 Species and sampling locations

Our sampling took into account all necto-benthic juvenile species encountered but not crypto-benthic species (Blenniidae, Gobiidae and Tripterygiidae). The study of the nursery value of *Cystoseira* forests (i.e. comparison of juvenile fish densities in *Cystoseira* vs. other natural habitats) was done in the Scandola Natural Reserve (NW Mediterranean, Corsica) (Fig. 1.1) where wide healthy *Cystoseira* forests can still be found. All infralittoral rocky habitats available in the study area were included in our surveys. We conducted a manipulative experiment studying the consequences of the depletion of *Cystoseira* forests in Villefranche Bay, France (Fig. 1.2).

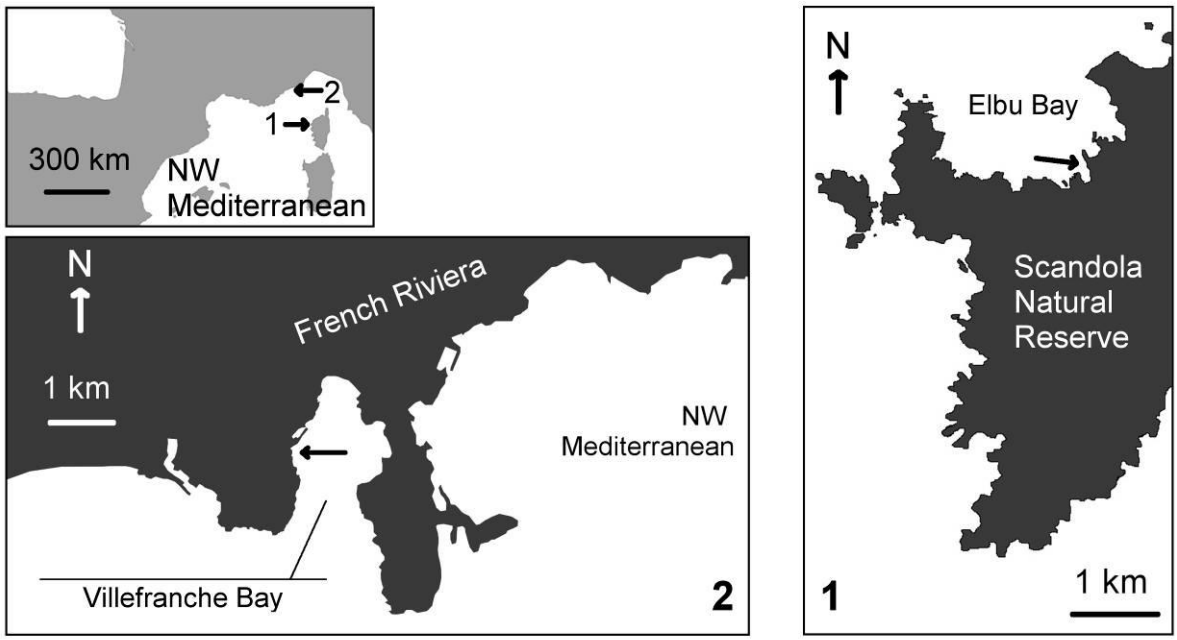

Fig. 1. Study locations (signaled by arrows). [1]Elbu Bay, Scandola Natural Reserve, Corsica: 42° 22' 17,07'' N, 8° 34' 18,26'' E (study of juvenile fish densities among natural habitats); [2]Villefranche Bay, southern France: 43° 41' 42,77'' N, 7° 18' 28,10'' E (manipulative experiment).

2.2 Quantifying the nursery value of Cystoseira *forests vs. different habitats*

In July and September 2009 we sampled two sites within Elbu Bay, Scandola Natural Reserve, containing wide superficies of each study habitats: the canopy forming *Cystoseira crinita* (Desf.) Bory forest and *Cystoseira brachycarpa* J. Agardh var. *balearica* (Sauvageau) Giaccone forests (hereafter *C. balearica* for simplicity), and a macroalgal assemblage dominated by others, not canopy-forming species (Dictyotales and Sphacelariales). Wide superficies of barren grounds were not present; therefore this habitat was not included in our study. The depth range of the study was between 2 and 4 meters, where settlement is commonly observed for Mediterranean coastal fish species (Francour and Le Direac'h, 1994; Garcia-Rubies and Macpherson, 1995; Guidetti and Bussotti, 1997; Harmelin-Vivien et al., 1995) and where *C. balearica* -and to a lesser extent- *C. crinita* have their optimum growth (Clarisse, 1984; Sales and Ballesteros, 2010). A SCUBA diver slowly swam and haphazardly selected 8 sampling points within each of the 3 studied habitats at each site. Substratum type (flat rock with few crevices) and slope (gentle, i.e. < 30°) were kept constant. At each sampling point the observer recorded macroalgal species percent coverage and mean canopy height (n = 8) in 1 m² plot (Francour and Le Direac'h, 1994; Garcia-Rubies and Macpherson, 1995).

We assessed the nursery value of each habitat measuring its first of four components (Beck et al., 2001) i.e. densities of juveniles per habitat area. During daylight (between 10am and 4pm), a diver used standard underwater visual census (UVC) techniques (Harmelin-Vivien et al., 1985) modified for juveniles (Francour, 1999; Francour and Le Direac'h, 2001) which allowed us to detect necto-benthic juveniles dwelling between macroalgae : the diver recorded the abundance and size of juvenile fishes within each 1m² plot at each sampling site during five minutes on a submersible plastic slate. The total length (TL) of individuals (±0.5 cm) was estimated with the help of fish silhouettes of different sizes on the slate and abundance was recorded per taxa per 5 mm size classes hereafter identified by their median (e.g. 12.5 mm = 10 – 15 mm size class) (Cheminée et al., 2011; Harmelin-Vivien et al., 1995; Vigliola et al., 1998). Rough sea and poor visibility days were avoided. Sampling was repeated twice during summer 2009 (July and September), at the middle and the end of the known settlement period for studied species (Table 0) (Froese and Pauly, 2011; Garcia-Rubies and Macpherson, 1995; Lejeune, 1984; 1985; Raventos and Macpherson, 2001). This period also follows the annual biomass maximum for most infralittoral macroalgal assemblages and more specifically *Cystoseira* species (Ballesteros, 1992; Hoffmann et al., 1992; Sales and Ballesteros, 2012). The smallest specimens of the species observed were considered newly settled individuals. For most rocky reef fishes in the Mediterranean, size at settlement is around 10 mm TL (Garcia-Rubies and Macpherson, 1995). Our visual censuses took into account the young of the year (juveniles, y_0 individuals) and also for some species size-classes that might correspond to young of the past year (y_{+1}) (see considered size range in Table 0 and Table 1 in Results).

Table 0
Theoretical reproductive schedule, pelagic larval phase duration (PLD) and settlement schedule of main studied species obtained or calculated from literature (Froese and Pauly, 2011; Lejeune, 1985; Raventos and Macpherson, 2001) and considered size-ranges during UVCs in the present study

	Reproduction schedule **x** = Lejeune (1985) ; **shaded area** = Froese & Pauly (2011)												**PLD (days)**		**Settlement schedule** calculated from reproduction schedule from Lejeune and with PLD from Lejeune (1985) (**x**) or PLD from Raventos & Macpherson (2001) (**shaded areas**)												**Studied size range in the present study (mm TL)**
Months	J	F	M	A	M	J	J	A	S	O	N	D	Lejeune (1985)[a]	Raventos & Macpherson (2001)[b]	J	F	M	A	M	J	J	A	S	O	N	D	
Taxa																											
Symphodus roissali				**x**	**x**	**x**	**x**						58 to 71	10 to 15						**x**	**x**	**x**	**x**					10 to 65
Symphodus tinca					**x**	**x**	**x**	**x**					-	10 to 11														10 to 65
Symphodus ocellatus							**x**	**x**	**x**	**x**	**x**		40 to 53	9 to 13								**x**	**x**	**x**	**x**			10 to 65
Coris julis					**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	26 to 45	21 to 34						**x**	**x**	**x**	**x**	**x**	**x**	**x**		10 to 65
Labrus merula													-	-														10 to 90
Labrus viridis													-	34														10 to 90
Serranus cabrilla													-	26														10 to 90
Serranus scriba													-	-														10 to 90

[a]based on the age of newly settled individuals calculated from their otoliths

[b]based on settlement marks of otoliths (lapilli) from post-settler individuals; author's remark: lapilli readings may induce an underestimation of this age (M. Harmelin-Vivien, pers. com.)

2.3 Experimental manipulation of Cystoseira *thalli densities and its consequences for fish juveniles*

To test the consequences of the decline of the *Cystoseira* forests on Mediterranean juvenile fish populations, we created artificial habitats mimicking various degrees of alteration of a *Cystoseira* forest in the bay of Villefranche (Fig. 1.2). This location displayed a similar environment than the previous one (Fig. 1.1) and logistical conditions better permitted a weekly monitoring.

In previous studies on seagrass habitat (Bell et al., 1987; Jelbart et al., 2006; Kenyon et al., 1999; Shulman, 1985; Worthington et al., 1991), as well as for Fucales (e.g. Sargassum) (Godoy and Coutinho, 2002; Ornellas and Coutinho, 1998; Shulman, 1985), artificial macrophytes use showed that they can attract assemblages of fishes similar to those found in natural habitats. Our hypothesis was that artificial plastic thalli mimicking *Cystoseira* spp. would attract fish assemblages similar to natural ones. The use of cultivated or harvested *Cystoseira*, or manipulation of natural forests, were not acceptable options due to their protected status and difficulties to cultivate it *ex-situ* (Susini et al., 2007). Prey densities for juvenile fish on plastic thalli may be lower than on natural thalli but (1) this putative artifact would be the same on each treatment and (2) this allowed to exclude the effect of food availability and to test only for the effect of tri-dimensional structure (i.e. refuge availability) on densities of fish juveniles. We used Artificial Sampling Units (ASU) mimicking 0.5 m² patches of *Cystoseira* forest[1]: square shaped plantation boxes provided the base of each ASU. ASUs were fixed to the seafloor with spits. Artificial plastic seaweeds provided by Pennplax® were used as Artificial *Cystoseira* (ACY). ACY were evenly distributed and fixed with concrete in plantation boxes to reproduce the canopy of a forest. The mean height of individual ACY stem was 17 cm (min = 12, max = 22, n = 30) and was constant among all ASUs. Each ACY was made of 5 stems. A half meter square patch was a relevant surface, wide enough to sustain juvenile fishes and small enough to permit accurate visual counts (authors' unpublished data).

The density of artificial *Cystoseira* cover was made of two levels: dense cover treatment (i.e. continuous cover with 160 ACY m^{-2}) and sparse cover treatment (i.e. non continuous cover with 48 ACY m^{-2}). This allowed us to mimic the natural cover of healthy *versus* depleted *Cystoseira* forests found in the upper Infralittoral in the NW Mediterranean (e.g. Corsica : E. Ballesteros, pers. comm.). Three ASU without artificial *Cystoseira* (bare concrete only) were monitored as control (control 2, C2). Plots of surrounding bare substratum of dead "matte" of the seagrass *Posidonia oceanica* were monitored as controls for ASU artifacts (i.e. attraction of fish by the ASU fixation system itself, Control 1). The dead matte was covered by a short turf composed of Dictyotales and Sphacelariales with 72% mean cover (Max: 80,

[1] See illustrations of ASU in Chapter IV-2 : photo panel A and B

Min: 60, n = 3) and 2.9 ± 0.3 (SE) cm mean height (n = 30). Each of the four cover treatments (Dense cover (D), Sparse cover (S), bare dead matte (C1), bare concrete (C2)) were repeated with 3 replicates (Fig. 2).

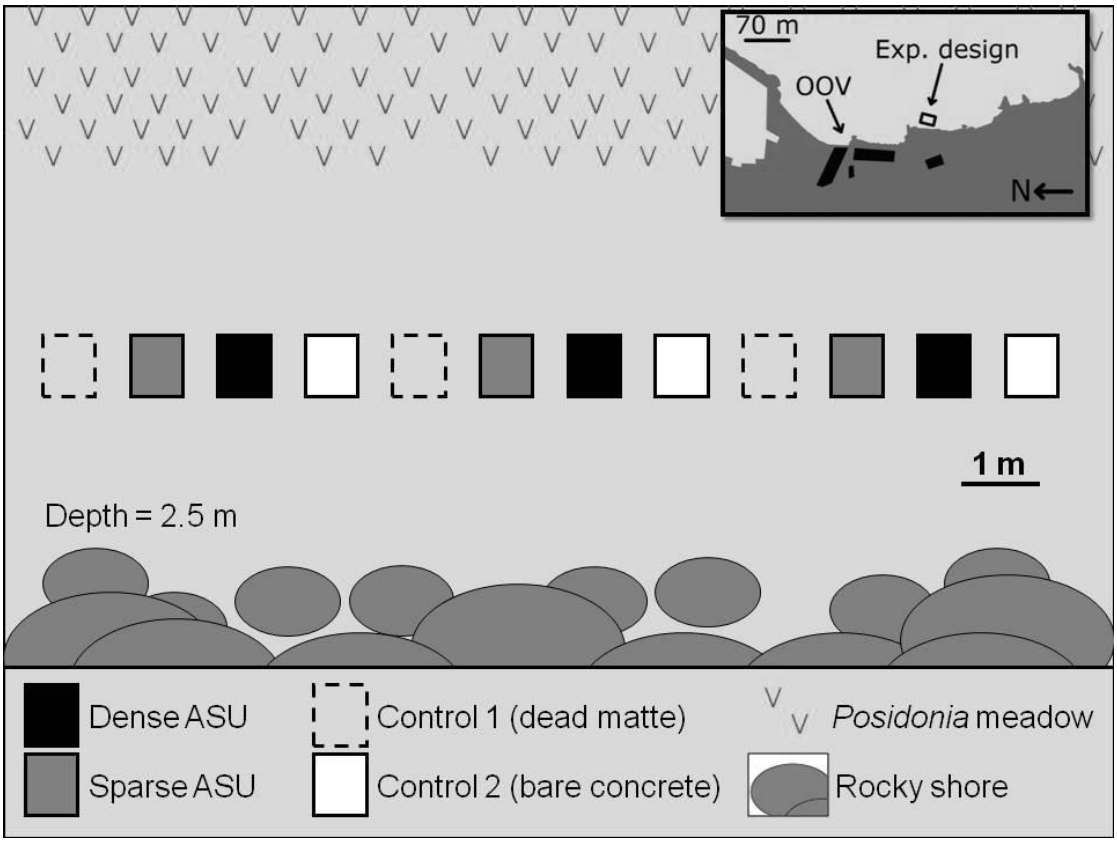

Fig. 2. Experimental design with three replicates of artificial sampling units for each of four treatments, and their exact position at the studied site within the Villefranche Bay (OOV: Oceanographic Observatory of Villefranche-sur-Mer).

Treatments were placed at 2.5 meters depth. Gently sloping surrounding bottoms had low macroalgal cover, with the same type of substratum made of bare dead "matte" of *Posidonia oceanica*. We chose this substratum because it provided the best conditions for fixing the experimental treatments (as opposed to rock, where fixing the ASUs was very difficult). However, we chose an area in the vicinity (within 5 meters) of rocky shores inhabited by the common NW Mediterranean infralittoral fish assemblages, to satisfy the initial hypothesis of an homogenous input of pelagic larvae (Lejeune, 1985) and to control for any influence of the natural habitat (Jelbart et al., 2006). ASU were at 0.5 meters from each others, in order to allow for fish movement between treatments and choice of habitat after settlement (Bell et al., 1987; Eckert, 1985). Orientation of all ASUs was identical.

ASUs were deployed at the beginning of spring 2009, in early April, before the beginning of the settlement period for most studied species, which takes place mainly between May and September (Garcia-Rubies and Macpherson, 1995; Raventos and Macpherson, 2001). This allowed artificial *Cystoseira* to gather epibiota and resemble the most possible to natural

thalli. From May to October, one diver (A. Cheminée) conducted weekly underwater visual censuses (upon meteorological conditions) to monitor density (ind. m^{-2}) of juveniles at each ASU, with the same method used in natural habitats.

2.4 Data analysis

2.4.1 Natural habitat data

Our hypothesis was that juvenile density would be higher in the two *Cystoseira* forests than in the Dictyotales and Sphacelariales assemblage. Total density per taxa and -for *Symphodus* spp. only- density per size classes were considered as variables.

Distribution of densities within our data contained many zeros and was highly skewed. Even after log-transformation it did not fit the normality assumption. In order to compare densities as a function of the various factors of our design, we thus decided to perform permutational univariate analysis of variance (PERANOVA) (Anderson, 2001) based on Euclidian distances measure (Terlizzi et al., 2007), which make this non parametric test the equivalent of a parametric ANOVA but free from the assumptions of normality and homoscedasticity of residuals (Anderson, 2001). P-values were obtained by 9999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). In order to compare densities between levels of factor (species, size class, habitat, site, month) we performed the PERANOVA on the model including terms and all interactions (Underwood, 1981). Terms were pooled as suggested by Anderson et al. (2008).

A first model was fit to total density per taxa in order to test the taxa-specific response of fish to habitat and month. Total juvenile density per taxa was modeled as a function of 4 factors: factor “taxa” has 4 levels (*Symphodus* spp., *Coris julis*, *Serranus* spp. and *Labrus* spp.) and is fixed; Factor “month” has 2 levels (July and September) and is fixed; Factor “habitat” has 3 levels (*Cystoseira crinita*; *Cystoseira balearica*; Dictyotales and Sphacelariales) and is fixed; Factor “site” has 2 levels, it is random and nested in Factor “habitat”. A second model was fit separately for *Symphodus* spp., considering density per size class. Juvenile abundances were pooled among three size classes: small (S) (12.5-27.5 mm TL), medium (M) (32.5-42.5 mm TL) and large (L) (47.5-62.5 mm TL). Putative effects of body size in fish relative to habitat and month were thus explored. This was not done for others taxa due to their lower abundances. In the second model, juvenile density per size class separately for each taxa was modeled as a function of 4 factors: factor “size classes” has 3 levels (small, medium and large) and is fixed; Factors “month”, “habitat” and “site” have the same characteristics than previously.

In order to compare habitat canopy height and coverage between levels of factor habitat and month we performed a PERANOVA as described previously. PERMDISP routine was applied to the same model in order to compare dispersion range of height and coverage

data around their median values (Anderson et al., 2008). Data treatment and analysis were performed using the R 2.15.0 statistical software (R_Development_Core_Team, 2012) and PERMANOVA+ add on package for PRIMER software (Anderson et al., 2008; Clarke and Gorley, 2006).

2.4.2 Experimental data

Our hypothesis was that for each week (weekly census from July to October) juvenile fish density (ind. m^{-2}) would be lower as macroalgal cover decreased. Cover treatments were Dense cover (D), Sparse cover (S), Control 1 = bare dead matte (C1) and Control 2 = bare concrete (C2). The experimental design was used to test the response of taxa-specific density of juveniles to weeks and treatments. We used the single size-class "Small+Medium" juveniles (12.5-42.5 mm TL for *Symphodus* spp. and 12.5-37.5 mm TL for *Coris julis*) and performed 2-factor ANOVA on juvenile densities. Juvenile density per taxa was modeled as a function of 2 factors: factor "time" (ti) (weekly census) has 17 (*Symphodus* spp.) and 12 (*Coris julis*) levels, is orthogonal and is fixed; Factor "cover treatment" (tr) has 4 levels, is orthogonal and is fixed. We tested for homogeneity of variance (Cochran's C test) and data transformations were used when necessary (Square root) (Underwood, 1997). When significant differences appeared among treatments we used post-hoc comparison test of Student-Newman-Keuls.

3. Results

3.1 Natural habitat characteristics

During the study period and within study sites, percent cover of both *Cystoseira* forests ranged from 80 to 100 %, while for the DS assemblage it ranged from 40 to 60 %. Erect strata height ranged from 11 to 22 cm for *C. crinita* and 7 to 18 cm for *C. balearica*, while it was always below 8 cm for the DS assemblage. For *Cystoseira crinita* and *C. balearica* canopy height and canopy cover, interaction terms between habitat and month were significant (Fig. 3; PERANOVA, respectively $F = 28.8$, $p < 0.001$ and $F = 13.9$, $p = 0.001$): for *C. crinita*, canopy height and percent cover were not different between July and September although dispersion of canopy height values was greater in September (Fig. 3; PERMISP, pair-wise test, $p = 0.014$) ; for *C. balearica*, both canopy height and percent cover were significantly lower in September than in July (pair-wise tests, both $p < 0.001$), without significant differences in dispersion of height or coverage values between months (PERMDISP, pair-wise tests, both $p > 0.05$). In July canopy height and canopy percent coverage slightly differed between both *Cystoseira* forests (PERANOVA, pair-wise tests, respectively $p = 0.037$ and $p = 0.011$) while in September *C. crinita* canopy height and canopy percent coverage were significantly much larger than for *C. balearica* (pair-wise test, respectively $p < 0.001$ and $p = 0.024$).

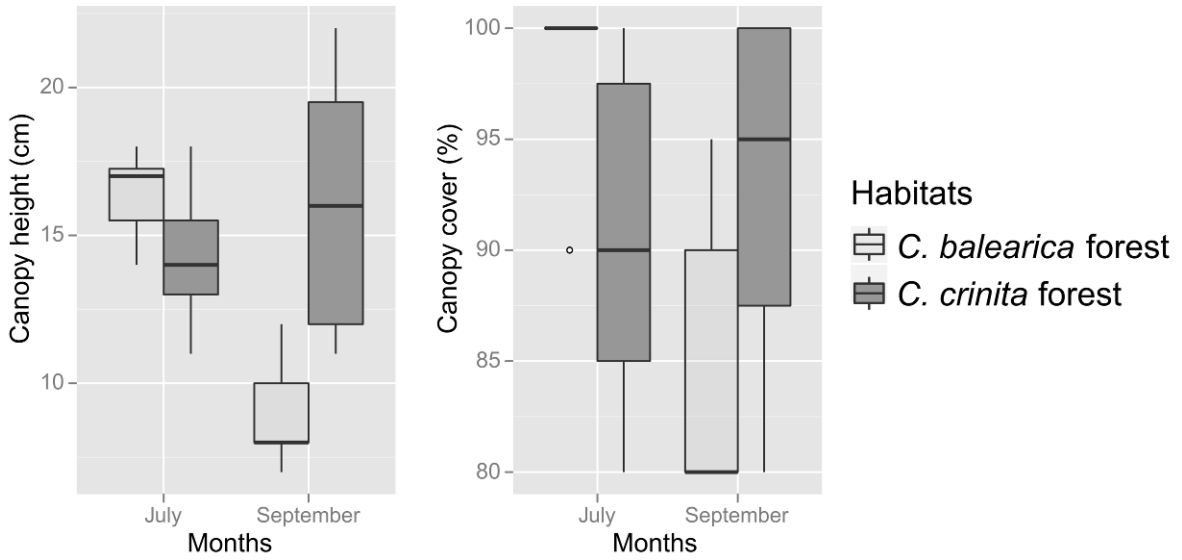

Fig. 3. *Cystoseira* spp. canopy height (cm) and cover (%) according to habitats and months ; see PERANOVA and PERMDISP results in section 3.1 ; height replicates per levels – Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles).

3.2 Settlement in natural habitats in Corsica

In the studied natural habitats in Corsica in 2009, 12 species of juveniles were seen associated with at least one of the two *Cystoseira* habitat and 8 species with the DS habitat (Table 1). Most frequent juveniles (i.e. taxa present in more than two replicates per site per month) belonged to species of the Labridae and Serranidae families: *Symphodus* spp. (i.e. including *S. roissali* (Risso, 1810), *S. tinca* (Linnaeus, 1758) and *S. ocellatus* (Forsskal, 1775)), *Coris julis* (Linnaeus, 1758), *Labrus* spp. (i.e. *L. merula* and *L. viridis* (Linnaeus, 1758)) and *Serranus* spp. (i.e. *S. cabrilla* and *S. scriba* (Linnaeus, 1758)). *Symphodus* species (particularly *S. ocellatus*) showed the highest settlers densities (Fig. 4). Occasional species (i.e. *Mullus surmuletus*, *Oblada melanura*, *Sarpa salpa*, *Thalassoma pavo* (Linnaeus, 1758)) and species that were dwelling in the water column (i.e. pelagic fish as Atherinidae) distinctly above the habitat and without interactions with it (e.g. hiding, feeding) were not included in the following results.

Table 1
Species and total number of species observed according to months and habitats (*Cystoseira crinita* (cr); *Cystoseira balearica* (ba); Dictyotales and Sphacelariales (DS) - Definitions of y_0 and y_{+1} size ranges

		Definitions of y_0 + y_{+1} size ranges	July			September		
			cr	ba	DS	cr	ba	DS
Frequent taxa	*Symphodus ocellatus* (Forsskal, 1775)	10 to 65	x	x	x	x	x	x
	Symphodus roissali (Risso, 1810)	10 to 65	x	x	x	x	x	x
	Symphodus tinca (Linnaeus, 1758)	10 to 65	x	x	x	x	x	x
	Coris julis (Linnaeus, 1758)	10 to 65	x	x	x	x	x	x
	Labrus spp. (i.e. *L. merula* and *L. viridis* (Linnaeus, 1758))	10 to 90	x	x		x		
	Serranus spp. (i.e. *S. cabrilla* and *S. scriba* (Linnaeus, 1758))	10 to 90	x	x	x	x	x	x
Occasional taxa	*Mullus surmuletus* (Linnaeus, 1758)	10 to 90	x		x	x		x
	Oblada melanura (Linnaeus, 1758)	10 to 90				x		
	Sarpa salpa (Linnaeus, 1758)	10 to 90		x	x			
	Thalassoma pavo (Linnaeus, 1758)	10 to 65					x	
Number of species			7	7	7	8	6	6

3.2.1 *Symphodus* species

In situ samples allowed to highlight the presence of *S. roissali*, *S. tinca*, and *S. ocellatus* among the *Symphodus* spp. juveniles; however, while performing UVC we could hardly distinguish these three species within the genus *Symphodus* due to their small sizes and because they shared the same habitats. As a consequence these three species were pooled together as *Symphodus* spp. for further analysis. In July, we recorded 159 *Symphodus* juveniles in the sampled 48 m² and their size distribution had modes at 22.5 and 37.5 mm TL. In September we recorded a total of 278 individuals, and their distribution had modes at 37.5 and 52.5 mm TL.

We described for *Symphodus* juveniles size class distribution per habitat because of their high abundances. In July, in *Cystoseira crinita* and *C. balearica* all 5 mm size classes from 17.5 to 57.5 mm TL were represented, with modes at 27.5 and 37.5 mm TL. Contrastingly, in the Dictyotales-Sphacelariales assemblage we observed fewer, isolated and only medium (32.5-42.5 mm TL) to large (47.5-62.5 mm TL) individuals. In September, in *C. crinita* and *C. balearica* all size classes from 17.5 to 62.5 mm TL were present with modes respectively at 22.5 and 52.5 mm TL, and 37.5 and 52.5 mm TL. Contrastingly, in the Dictyotales-Sphacelariales assemblage we observed only large individuals.

3.2.2 Other species: *Coris julis*, *Serranus* spp. and *Labrus* spp.

In July, an assemblage of few *Coris julis* juveniles was visible over all facies (among 48 m², 19 individuals from 17.5 to 42.5 mm TL and mode at 27.5 mm TL). In September the assemblage included more numerous individuals (80 ind. distributed from 32.5 to 62.5 mm TL and mode at 42.5 mm TL). For *Serranus* spp. and *Labrus* spp., observed individuals were isolated and abundances of juveniles (12.5-87.5 mm TL) were low: respectively 18 and 11 individuals for July and 21 and 3 individuals for September.

3.3 Densities of juvenile fishes in natural habitats

The different taxa had different density patterns among habitats (Fig. 4). Total *Symphodus* densities differed between habitat (PERANOVA, $F = 31.5$, $p < 0.001$) and were significantly larger in *Cystoseira balearica* (mean ± S.E., 7.5 ind. m^{-2} ± 0.9) than in *C. crinita* (5.5 ind. m^{-2} ± 0.8) ($p = 0.070$), and larger in *C. crinita* than in Dictyotales and Sphacelariales (DS) (0.6 ind. m^{-2} ± 0.2) ($p < 0.001$) (Fig. 4a and see Appendix #2a for PERANOVA tables). Total *Symphodus* densities were also significantly larger in September (5.8 ind. m^{-2} ± 0.8) than in July (3.3 ind. m^{-2} ± 0.5) (PERANOVA, $F = 11.4$, $p < 0.001$). The density on each of the *Symphodus* size classes was significantly different between months and habitats (Fig. 4e). In both July and September, for each size class, *Symphodus* juvenile densities were significantly larger in *C. crinita* and *C. balearica* habitats than in DS (Fig. 4e; see Appendix #2b for pair-wise comparisons). In July there were no significant differences in *Symphodus* density between *C. balearica* and *C. crinita*. In September, "small" juveniles (12.5-27.5 mm TL) were significantly more abundant in *C. crinita* than in *C. balearica* (pair-wise test, $p = 0.016$); for "medium" and "large" juveniles (32.5-62.5 mm TL), densities were significantly larger in *C. balearica* than in *C. crinita* (pair-wise tests, $p = 0.002$ and $p = 0.028$ respectively).

Total density of *Coris julis* was significantly different among habitats (PERANOVA, $F = 11.5$, $p < 0.001$). In July (Fig. 4b) *Coris* densities did not differ among habitats while in September *Coris* densities were significantly higher in DS than in *C. balearica* (pair-wise test, $p = 0.003$), significantly higher in *C. balearica than* in *C. crinita* (pair-wise test, $p = 0.045$), and significantly higher in DS than in *C. crinita* (pair-wise test, $p < 0.001$). In DS and *C. crinita* densities did not differ between July and September (pair-wise test, $p > 0.1$) while in *C. balearica Coris* densities were significantly larger in September than in July (pair-wise test, $p = 0.045$).

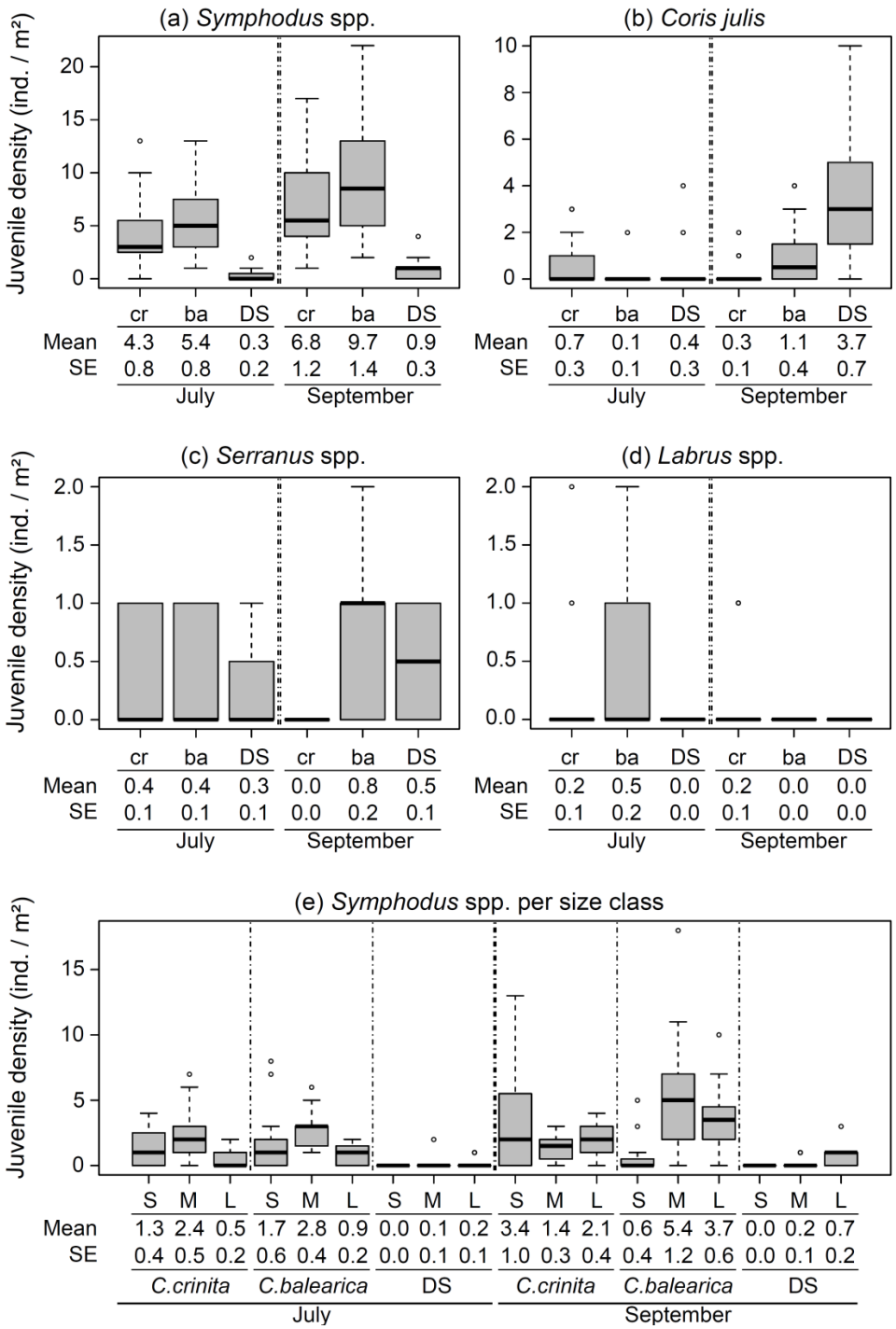

Fig. 4. Juvenile densities per taxa among studied natural habitats (treatments) and months; treatments = *Cystoseira crinita* (cr), *Cystoseira balearica* (ba), Dictyotales and Sphacelariales (DS); (e): *Symphodus* spp. juvenile densities per size class among habitats and months, size class = S (small, 12.5-27.5 mm TL), M (medium, 32.5-42.5 mm TL) and L (large, 47.5-62.5 mm TL).; see PERANOVA tables and pair-wise tests in Appendix # 2a & 2b – Box plots indicate the median (bold line near the center), the first and third quartile (the box), the extreme values whose distance from the box is at most 1.5 times the inter quartile range (whiskers), and remaining outliers (open circles) – Mean density (ind. m^{-2}) and standard error (SE) are indicated below graphs for each taxa per habitat and per season.

For total density of *Labrus* spp., interaction term between month and habitat was significant (PERANOVA, $F = 4.7$, $p < 0.05$): in July (Fig. 4d) densities were significantly larger in *C. balearica* than in DS (pair-wise test, $p = 0.004$) while in September densities were too low to allow us to make conclusions.

For *Serranus* spp. densities (Fig. 4c), interaction term between month and habitat (PERANOVA, $F = 6.4$, $p = 0.003$) was significant but few differences appeared between habitats: in September, total densities were almost significantly higher in DS than in *C. crinita* (pair-wise test, $p = 0.060$).

3.4 Assemblages and densities of juveniles observed in Artificial Sampling Units

We only present here results for the two most frequent taxa (*Symphodus* spp. and *Coris julis*). The first *Symphodus* spp. juveniles on the experimental plots (ASUs) were first observed on July 1, 2009 (18.75 mm mean TL, max: 22.5, min: 12.5, n = 4) (Fig. 5a). At the end of the monitoring period (October 9) the *Symphodus* juvenile assemblage on the 12 ASUs (6 m²) comprised 21 individuals (27.5 – 57.5 mm TL, mode: 32.5 mm TL). During the first half of the monitoring period (from early July to mid August) juveniles were quite cryptic, and either solitary or in groups of 2-3 individuals; from mid August to early October juveniles became less cryptic and tended to form larger schools of 3 up to 11 individuals on top of the ASUs'canopy.

For *Symphodus* spp. juvenile densities, interaction term between time and treatment was significant (ANOVA, $F = 1.9$, $p < 0.01$) and densities were significantly larger in Dense and/or Sparse treatments than in bare concrete and bare dead matte treatments during the entire study period (Fig. 5b): during the first part of the monitoring (from early July to mid August) more than half of censuses (56%) showed significantly larger densities for Sparse treatments only, while later on (from mid-August to early October) densities were significantly larger for both Dense and Sparse treatments for 88% of the times (Fig. 5b).

In the case of *Coris julis*, a first solitary juvenile (27.5 mm TL) was observed on July 30. Smaller individuals were observed later (22.5 mm, August 4; 17.5 mm, August 14) and regularly until the end of the monitoring period. *Coris* juveniles were mostly solitary individuals or in pairs. When present on Dense or Sparse treatments, *C. julis* was often observed at the edge of the forest.

For *Coris julis* densities, the treatment term was significant (ANOVA, $F = 3.03$, $P = 0.033$) but the interaction term between time and treatments was not significant (ANOVA, $F = 1.14$, $P = 0.307$); *Coris* densities on bare dead matte (C1, 1.2 ± 0.3 (SE) ind. m^{-2}) were significantly larger than on Dense cover treatment (0.3 ± 0.1 (SE) ind. m^{-2}) (SNK, $0.01 < p < 0.05$) but did not significantly differ from densities on Sparse cover (0.9 ± 0.2 (SE) ind. m^{-2}) or bare concrete (C2, 0.6 ± 0.2 (SE) ind. m^{-2}) treatments.

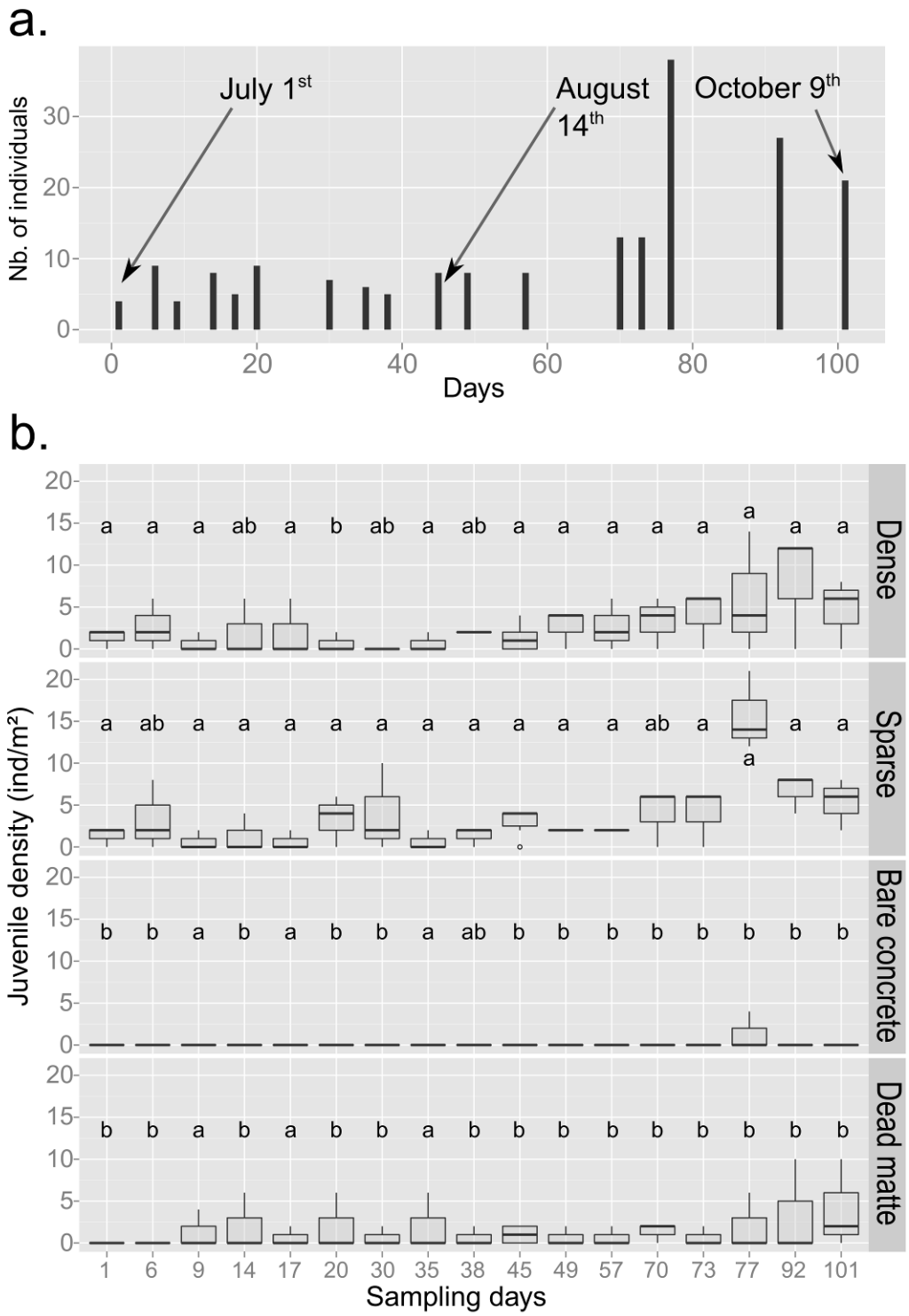

Fig. 5. (a): total abundance through time of *Symphodus* spp. juveniles (12.5-42.5 mm TL) over the 12 ASUs in 2009; (b): boxplots of *Symphodus* spp. (12.5-42.5 mm TL) densities (ind. m^{-2}) per treatments and per sampling days from July to October 2009; For each sampling days, between-treatment comparisons (SNK post-hoc test results) are given (different lower case characters indicate significant differences between treatments) – boxplot legend as in Fig. 4.

4. Discussion

4.1 Nursery value of Cystoseira *forests for juvenile fishes*

Our study shows that in shallow rocky bottoms of the NW Mediterranean, *Cystoseira* forests are important nurseries for some species of littoral fishes including species of commercial interest for recreational and professional fisheries. Our observations in both natural habitats and experimental plots showed that the complex – sensu August (1983) – canopy-forming *Cystoseira* forests had a high nursery value -*sensu* Beck et al. (2001)- for the abundant *Symphodus* species (*S. ocellatus*, *S. roissali*, *S. tinca*), as juvenile densities where larger in both *C. crinita and C. balearica* habitats than in alternate states without the *Cystoseira* canopy i.e. other erect macroalgae or bare substratum. Moreover, this nursery value was consistent through the settlement-recruitment period for these species. Although we were not able to distinguish between the different *Symphodus* species *in situ*, it was quite clear that the same forests were used successively through time by these three species and by successive cohorts of settlers of each species. This was illustrated by observed modes and the significantly larger densities (including small sized individuals) observed in September than in July. The additional young settlers probably belonged to *Symphodus ocellatus* species, which is known to settle latter than *S. roissali* and *S. tinca* (Garcia-Rubies and Macpherson, 1995; Lejeune, 1985), while the larger individuals observed in September may correspond to these last two species.

Coris julis, in contrast, was observed more frequently in the Dictyotales-Sphacelariales habitat than in both *Cystoseira* forests, as well as more frequently in the experimental treatments without a canopy; when present on the canopy treatments it was mostly in the sparse forest and besides was commonly observed near the edge of the forest. Garcia-Rubies and Macpherson (1995) found *Coris* juveniles mostly associated with open plots of sandy bottoms but reported that they likewise settled onto *Posidonia oceanica* beds. At ecotones, juveniles may forage in non-canopy habitats and shelter within the arborescent cover (macroalgae or seagrass). This might be an expression of the "edge effect" (Baker et al., 2002). However, our results do not allow us to conclude that the *Cystoseira* canopy is essential for *Coris* juveniles.

In our study juveniles of *Serranus* spp. showed no density differences between habitats, in agreement with Garcia-Rubies & Macpherson (1995) results. This is probably due to their "stalk-and-attack" predator behavior (Savino and Stein, 1989) that justify the fact that they swim through various habitats in order to actively look for preys[2]. Individuals have been observed e.g. standing by the edge of a canopy forming habitat before to run and hit a small *Symphodus* juvenile dwelling in the forest (authors' unpublished data). La Mesa et al. (2002)

[2] See Chapter III-part 5 for more information on predator types

showed that juveniles of both *S. scriba* and *S. cabrilla* preferred open, not sheltered habitats, suggesting that they do not need canopy protection.

For *Labrus* spp., in July, juveniles were more abundant on the *Cystoseira balearica* canopy. However, the lower abundances of observed *Labrus* (n = 3) in September did not allow us to confirm such pattern. Other authors mention that young *Labrus* individuals are seen more often in *Posidonia oceanica* seagrass meadows than on bare rocky bottoms (Louisy, 2005). Garcia-Rubies & Macpherson (1995) showed that juveniles of *L. merula* and *L. viridis*, although characteristic of rocky bottoms, exhibited some affinities for isolated clumps of *Posidonia oceanica*.

In agreement with previous studies on other erect canopy-forming macroalgae elsewhere in temperate seas (Aburto-Oropeza et al., 2007; Carr, 1989; 1994; Jones, 1984) or in the Mediterranean (Garcia-Rubies and Macpherson, 1995), our study quantified and highlighted for the first time the high nursery value of *Cystoseira* forests relatively to other rocky habitats; Riccato et al. (2009) found a significant positive correlation between the biomass of macroalgae covering rocky bottoms (made up of *Cystoseira barbata* and *C. compressa*) and the abundances of two fish species, *Symphodus roissali* and *Diplodus annularis*. However they did not distinguish between adult and juvenile fish. Their hypothesis was that erect canopy-forming *Cystoseira* species provided food and shelter, thus offering more ecological niches for fish species. Among erect macrophytes of the Mediterranean, the high nursery value and consequent nursery role of *Posidonia oceanica* meadows for some species (*Diplodus annularis*, *Spondyliosoma cantharus*, and Sy*mphodus cinereus*) has also been indicated (Francour and Le Direac'h, 1994; Garcia-Rubies and Macpherson, 1995; Guidetti, 2000; Guidetti and Bussotti, 1997; Harmelin-Vivien et al., 1995; Le Direac'h and Francour, 1998). However, Garcia-Rubies & Macpherson (1995) stated that this habitat supports few species in comparison with rocky substrates, particularly those bearing canopy-forming macroalgae. To date no studies have been published comparing the nursery value of seagrass beds *vs*. canopy-forming macroalgae on rocky bottoms.

4.2 Factors that determine the nursery value of Cystoseira *canopies*

Several processes may explain juvenile abundance differences between habitats (Beck et al., 2001; Harmelin-Vivien et al., 1995; Olabarria et al., 2002b). First, the pelagic larval input may be different between locations (Beck et al., 2001; Vigliola et al., 1998). Second, density differences may be explained by differential mortality of juveniles among treatments, due to highest survival in the more complex canopy forming habitat because of a) lower predation rate due to a higher amount of refuges available (Juanes, 2007; Piko and Szedlmayer, 2007) or b) better nutrition due to greater amount of food items. Finally, these differences may be induced by an active choice of habitats by juveniles (Bell and Westoby, 1986), selecting the habitat which provides them the best compromise according to predation rates and food availability (Dahlgren and Eggleston, 2000; Horinouchi et al., 2009b).

However, our experimental study was designed so that all experimental treatments were supposed to receive the same input of settlers. Moreover, according to previous studies, *Symphodus ocellatus* juveniles eat mostly planktonic, epibenthic and bentic meiofauna (e.g. copepods) commonly present near or on the substratum and within all studied habitats (Levi, 2004). Besides, our artificial thalli attracted juvenile assemblage qualitatively similar to natural ones. Food items may thus not be a limiting factor and may not be the main factor influencing habitat nursery value. Consequently, according to our results and previous studies, we believe that refuge availability is the main driver of the nursery value of *Cystoseira* forests. The presence of a canopy i.e. a complex tri-dimensional structure may offer better protection to juveniles from predators. Juvenile density differences may consequently be the result of either an active choice by the juveniles of the habitat presenting more refuges, or differential mortality among various habitats because of different refuge availabilities.

When considering the *Symphodus* spp. density per size class, in July, small, medium and large juveniles had the same pattern of habitat use (i.e. [*C. balearica*] = [*C. crinita*] > [DS]) but in September small juveniles were more numerous in *Cystoseira crinita*, when medium and large individuals were more numerous in *C. balearica* ; moreover few and only large individuals were dwelling into the DS, less complex habitat. Previous studies in Corsica about seasonal changes in the biomass naturally occurring in macroalgal assemblages highlighted that *Cystoseira balearica* loses a large proportion of its branches twice a year, including between June and October (Hoffmann et al., 1992) which suggests that in September *C. balearica* may have a less complex canopy. Our canopy height and coverage data confirmed this trend, which may explain the juvenile density patterns we observed: the shorter and sparser *C. balearica* canopy in September compared to *C. crinita* may indeed provide e.g. fewer refuges and be less suitable for the small size-class juveniles, particularly susceptible to predation. Similarly, only large juveniles may dare to dwell into the open DS habitat. Ontogenetic habitat shift from macroalgal forest to less complex surrounding habitat has been observed previously for example for the Nassau grouper *Epinephelus striatus* and were interpreted as behavioral responses aiming at minimizing the ratio of mortality risk to foraging efficiency (Dahlgren and Eggleston, 2000). Moreover, in order to disentangle whether active movement from one forest to the other or differential mortality of different size-class individuals resulted in the observed patterns, more research is required e.g. analyzing the connectivity between the studied habitats. Previous works (Clarisse, 1984; Sales and Ballesteros, 2010) highlight that *C. crinita* and *C. balearica* are often found successively along a depth gradient, i.e. *C. crinita* is mostly restricted to shallow (0-3 meters) waters while *C. balearica* replaces it in deeper waters (2-9 meters). Moreover they observe *C. crinita* to be restricted mostly to sheltered areas. If so, connectivity between both forest types may be low and if juvenile patterns as we observed repeat themselves in other areas where forest are clearly not connected, it might rather result from differential mortality

more than from movement from one type of forest to the other. Dispersal capabilities of juveniles (home range) deserve as well more research.

4.3 Consequences of the depletion of Cystoseira *forests*

Cystoseira crinita and *C. balearica* canopies in our study site support in average respectively 9 and 12 times more juveniles of *Symphodus* spp. than habitats with less complexity, suggesting that the historical and current depletion of *Cystoseira* forests in the NW Mediterranean and the Eastern Mediterranean (Mangialajo et al., 2007; Sala et al., 2011; Thibaut et al., 2005) may have already had significant consequences for the replenishment of littoral fish populations in the region.

In the NW Mediterranean, *Cystoseira* forests have disappeared because of a combination of factors including human trampling, chemical pollution, mechanical destruction by land claiming, increased water turbidity, dominance by invasive species, overfishing of sea urchin predators (mostly Sparidae and Labridae fishes) and the consequent overgrazing by sea urchins through trophic cascades (Ballesteros et al., 2002; Guidetti, 2004; Pinnegar et al., 2000; Sala et al., 1998; Thibaut et al., 2005). In the Eastern Mediterranean, *Cystoseira* forests are also threatened by large abundance of two Lessepsian herbivorous fish from the Red Sea (*Siganus luridus* and *S. rivulatus*), which are responsible for the creation and maintenance of barren grounds (Sala et al., 2011). These alien species have been recently reported in the NW Mediterranean, from a few individuals (Daniel et al., 2009) up to schools of hundred individuals (fall 2011, H. Molenaar, pers. comm.). New oceanographic conditions and increasing warming of surface seawater could facilitate the spreading of Lessepsian species towards the western basin (Bodilis et al., 2011) and contribute to the depletion of macroalgal canopies.

Algal assemblages without canopy and barrens may not be able to play a nursery role as *Cystoseira* forests, thus lowering the recruitment of coastal fish assemblages. On rocky bottoms of Corsica, it is common to observe large and continuous forest of *Cystoseira balearica* covering more than 2500 m². According to our results the depletion of such forests potentially means the loss of about 22000 *Symphodus* spp. juveniles. Although to a lesser extent, *Labrus*, *Serranus*, and *Coris* juveniles seemed to rely as well on *Cystoseira* forests, notably through edge effects e.g. for foraging activities (*Serranus*) or sheltering (*Coris*). *Symphodus* spp., *Labrus* spp*. and Serranus* spp. are species with commercial interest which belong to typical Mediterranean cooking specialties (e.g. for fish soup, sold on market about 10 to 15 Euros per Kg). Lowered forest's nursery value and consequent depletion of these populations is therefore of serious concern for conservation and coastal fisheries management. In the present study, in artificial sampling units mimicking the alteration of a *Cystoseira* forest, assemblage composition of juveniles observed in Dense patches were similar to those in natural forests. Our results showed that there were no artifacts associated with the bases used for anchoring the experimental canopies: since bare concrete ASU and

bare dead matte substratum did not differ in abundances of juveniles we can infer that juveniles were attracted by Dense and Sparse ASU because of the presence of a canopy and not by the concrete base. These elements justify the use and design of our artificial habitats. However, no differences were found between Dense and Sparse cover treatments for *Symphodus* spp. juveniles. Therefore we were not able to determine the threshold canopy cover at which fish settlement and recruitment collapses (Bell et al., 1987; Worthington et al., 1991). More research is needed to determine that threshold, to test for patch size effect, and also to test the effects of the *Cystoseira* canopy on the entire fish assemblage and other shallow species with key ecological roles and commercial importance (e.g., *Epinephelus marginatus*, *Diplodus sargus*).

CONCLUSION

As a conclusion, this study highlighted and quantified for the first time the high nursery value of *Cystoseira* forests for some species of littoral fishes of ecological and economical importance. Our observations in both natural and manipulated habitats suggested that refuge availability was the main driver of forests nursery value. Our results suggested that the loss of these forests may strongly affect the recruitment of these fishes. Furthermore, at a seascape scale in shallow rocky bottoms of the NW Mediterranean, we also believe that a mosaic of habitats may be more productive than a single habitat, due to complementarities of habitats (as illustrated by the different distribution patterns of *Symphodus* and *Coris*) and synergies between habitats (as illustrated by edge effects). These processes acting at the seascape scale require as well more research and the current legal framework of coastal management may have to upgrade from a habitat perspective toward a seascape perspective.

ACKNOWLEDGMENTS

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APPENDIX

Appendix #2a
PERANOVA table of juvenile densities per taxa in natural habitats - main tests

Factor "size class" (sc) has 3 levels (small (S), medium (M) and large (L))
Factor "month" (mo) has 2 levels (July and September (sept))
Factor "habitat" (ha) has 3 levels (*Cystoseira crinita* (cr); *Cystoseira balearica* (ba); Dictyotales and Sphacelariales (DS))
Factor "site" (si) has 2 levels and is nested in Factor "habitat"

Taxa considered	Source of var.	df	MS	Pseudo-F	*P* (perm)	
All taxa	Taxa (ta)	3	401.93	102.74	0.0001	***
	Habitat (ha)	2	72.44	18.52	0.0001	***
	Month (mo)	1	79.75	20.39	0.0001	***
	taxha	6	120.54	30.81	0.0001	***
	taxmo	3	35.76	9.14	0.0001	***
	haxmo	2	6.25	1.60	0.2036	n.s.
	taxhaxmo	6	17.64	4.51	0.0006	***
	Pooled (si(ha), taxsi(ha), si(ha)xmo, taxsi(ha)xmo, Res)	360	3.91			
	Total	383				
Symphodus spp. total	ha	2	408.04	31.50	0.0001	***
	mo	1	147.51	11.39	0.0005	***
	haxmo	2	28.17	2.17	0.1210	n.s.
	Pooled (si(ha), moxsi(ha), Res)	90	12.95			
	Total	95				
Coris julis	ha	2	24.13	11.49	0.0001	***
	mo	1	38.76	4.93	0.1067	n.s.
	haxmo	2	28.79	3.66	0.1435	n.s.
	si(ha)xmo	3	7.86	3.74	0.0129	*
	Pooled (si(ha), Res)	87	2.10			
	Total	95				
Serranus spp.	ha	2	1.34	1.68	0.3323	n.s.
	mo	1	0.09	0.39	0.5309	n.s.
	si(ha)	3	0.80	3.34	0.0236	*
	haxmo	2	1.53	6.37	0.0025	**
	Pooled (moxsi(ha), Res)	87	0.24			
	Total	95				
Labrus spp.	ha	2	0.54	3.79	0.0214	*
	mo	1	0.67	4.66	0.0290	*
	haxmo	2	0.67	4.66	0.0103	*
	Pooled (si(ha), moxsi(ha), Res)	90	0.14			
	Total	95				

Symphodus spp. by size classes	ha	2	136.01	37.30	0.0001	***
	mo	1	49.17	13.49	0.0002	***
	sc	2	21.25	5.83	0.0035	**
	haxmo	2	9.39	2.58	0.0759	·
	haxsc	4	29.87	8.19	0.0001	***
	moxsc	2	11.69	3.21	0.0392	*
	haxmoxsc	4	24.54	6.73	0.0001	***
	Pooled (si(ha), moxsi(ha), si(ha)xsc, moxsi(ha)xsc, Res)	270	3.65			
	Total	287				

n.s., not significant

· $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

P-values were obtained by 9999 permutations of residuals under a reduced model

Appendix #2b

Pair-wise comparisons conducted after PERANOVAs of juvenile densities per taxa in natural habitats

Legend as in Appendix #2a

Taxa considered	Term or Levels		Groups	t	*P*	
Symphodus spp. total		Term 'ha (habitat)'	cr, ba	1.832	0.0729	.
			cr, DS	6.604	0.0001	***
			ba, DS	8.429	0.0001	***
		Within level 'july' of factor 'month'	cr, ba	0.941	0.3562	n.s.
			cr, DS	4.567	0.0002	***
			ba, DS	5.925	0.0001	***
		Within level 'sept' of factor 'month'	cr, ba	1.573	0.1323	n.s.
			cr, DS	4.860	0.0002	***
			ba, DS	6.263	0.0001	***
Coris julis		Term 'ha'	cr, ba	0.507	0.6261	n.s.
			cr, DS	3.912	0.0003	***
			ba, DS	3.451	0.0012	**
		Within level 'july' of factor 'month'	cr, ba	1.893	0.0678	.
			cr, DS	0.816	0.4223	n.s.
			ba, DS	0.835	0.4059	n.s.
		Within level 'sept' of factor 'month'	cr, ba	2.100	0.0453	*
			cr, DS	4.559	0.0001	***
			ba, DS	3.191	0.0034	**
Labrus spp.		Term 'ha'	cr, ba	0.540	0.5954	n.s.
			cr, DS	2.216	0.0303	*
			ba, DS	3.162	0.0019	**
		Within level 'july' of factor 'month'	cr, ba	1.499	0.1408	n.s.
			cr, DS	1.379	0.1802	n.s.
			ba, DS	3.162	0.0037	**
		Within level 'sept' of factor 'month'	cr, ba	1.861	0.0770	·
			cr, DS	1.861	0.0709	·
			ba, DS	Den. is 0		
Serranus spp.		Within level 'july' of factor 'month'	cr, ba	Negative		
			cr, DS	1.000	0.4229	n.s.
			ba, DS	1.000	0.4300	n.s.
		Within level 'sept' of factor 'month'	cr, ba	2.600	0.1258	n.s.
			cr, DS	4.000	0.0600	.
			ba, DS	0.928	0.4535	n.s.
Symphodus spp. per size	Within level	Within level 'S' of	cr, ba	0.528	0.6073	n.s.

class	'july' of factor 'month'	factor 'sc'	cr, DS	3.626	0.0010	**
			ba, DS	2.764	0.0092	**
		Within level 'M' of factor 'sc'	cr, ba	0.632	0.5160	n.s.
			cr, DS	4.717	0.0001	***
			ba, DS	7.121	0.0001	***
		Within level 'L' of factor 'sc'	cr, ba	1.464	0.1538	n.s.
			cr, DS	1.667	0.1095	n.s.
			ba, DS	3.051	0.0060	**
	Within level 'sept' of factor 'month'	Within level 'S' of factor 'sc'	cr, ba	2.557	0.0157	*
			cr, DS	3.322	0.0017	**
			ba, DS	1.775	0.0842	.
		Within level 'M' of factor 'sc'	cr, ba	3.334	0.0019	**
			cr, DS	4.314	0.0002	***
			ba, DS	4.409	0.0002	***
		Within level 'L' of factor 'sc'	cr, ba	2.276	0.0278	*
			cr, DS	3.352	0.0029	**
			ba, DS	4.627	0.0001	***

n.s., not significant

. $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

P-values were obtained by 9999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<1000).

REFERENCES

See Chapter “References”

3.3 Supplementary data: Spatial and temporal variability of fish juvenile densities within Cystoseira forests and Dictyotales - Sphacelariales bushland - preliminary results

3.3.1 Introduction

Thistle et al. (2010) showed that juvenile fishes associated with eelgrass *Zostera marina* displayed variable densities according to site and the scale of analysis. Vigliola et al. (1998) showed a strong temporal (between year) and spatial (among 20 NW Mediterranean sites) variability of three *Diplodus* species settlement intensity. Our study (previous part) of *Cystoseira* forests nursery value was done in one natural habitats site (a cove in Scandola Natural Reserve, Corsica) and during one year (July and September 2009). Consequently the first objective of the present part aimed at:

- (1) assessing if the observed higher juvenile densities in *Cystoseira* forest in comparison with the Dictyotales – Sphacelariales (DS) bushy habitat was consistent through space (at scales of 1, 10 and 20 kilometers) and through time (between at least two consecutive years).

Besides, for *Cystoseira balearica* forests only, sampled between 3 to 8 meters over gently sloping continuous rocky bottoms, in areas displaying similar adult fish assemblages, we hypothesized that the spatial variability of its fish juvenile densities would be modulated by the other non-controlled abiotic or biotic factors such as exposure or slight differences in slope, depth and canopy height. We furthermore hypothesized that residuals variability, if any, must then be explained by variability in larval input (see discussion in part 3.2), which until now we considered homogenous at a local scale but which may be heterogeneous over wider spatial scale for example due to oceanographic current patterns. If this is the case, this residual variability must be quantified since it has conservation implications: not only nursery habitat must be protected in one place, but rather in a network of spatially dispersed places in order to prevent for local failure in settlement. Consequently the second objective of this part was:

- (2) to study the spatial variability of juvenile densities within *Cystoseira balearica* forests and its correlation with environmental (biotic and abiotic) factors.

Here I present only some supplementary available data from our campaign performed during my second year of PhD, during the summer 2010, as preliminary results; we aim at presenting the full study in a paper (in prep.) for publication.

3.3.2 Material and methods

For this study I selected respectively 13 and 10 sites in two large bays situated in two locality of Corsica (NW Mediterranean): the bay of la Revellata and Calvi Gulf on one hand, and the bay of Elbu in the Natural Reserve of Scandola on the other hand (Fig. 1). Both localities are located at 20 km apart from each other, along the North-west coast of Corsica. First, in order to select the study sites, I explored by snorkeling the shallow (0-10 meters) habitats along the 5 km coast of Elbu Bay (June 2009) and the 5 km coast of la Revellata Bay (September 2009). In both case I schematically mapped the micro-habitats of the entire explored area (substrate type, biotic cover, slope, depth). This micro-habitats localization was completed in july 2010 in La Revellata by punctual *in situ* observations (A. Cheminée and J. Pastor) and with unpublished data of K. Ballesteros, J.-M. Dominici, P. Lejeune, C. Pelaprat, and A. Chery.

Based on these data, during the summer 2010 I was able to select for each locality a set of sites each containing both wide *Cystoseira balearica* forest and DS bushland (as described in the part 3.2). These study sites (Fig. 1) were selected so that all other micro-habitat biotic and abiotic characteristics were kept as constant as possible: percentage of canopy cover above 70% (for *C. balearica*) and 40% (for DS), continuous rock, gentle (0-23°) or pronounced (23-45°) slope only - *sensu* Bariche et al. (2004) - , shallow depth (2-8 meters). Other, non-controlled, factors included exposure against swell and canopy height.

From July 14th to August 8th 2010, in each site, in each habitat, 7 replicates of 1 m² were randomly selected. In each square meter the same divers (A. Cheminée and J. Pastor in la Revellata; AC, O. Bianchimani, J.-M. Cottalorda in Scandola), previously inter-calibrated, performed 5 minutes underwater visual censuses of juvenile fishes as described in the previous part. Micro-habitat characteristics (slope, depth, exposure, canopy height and percent cover) were recorded in each replicate plot (see factor modalities hereafter).

It is worth noting that “ELE” site in Elbu Bay, included in this campaign (2010), was one of the two sites studied in 2009 in the previous paper (part 3-2).

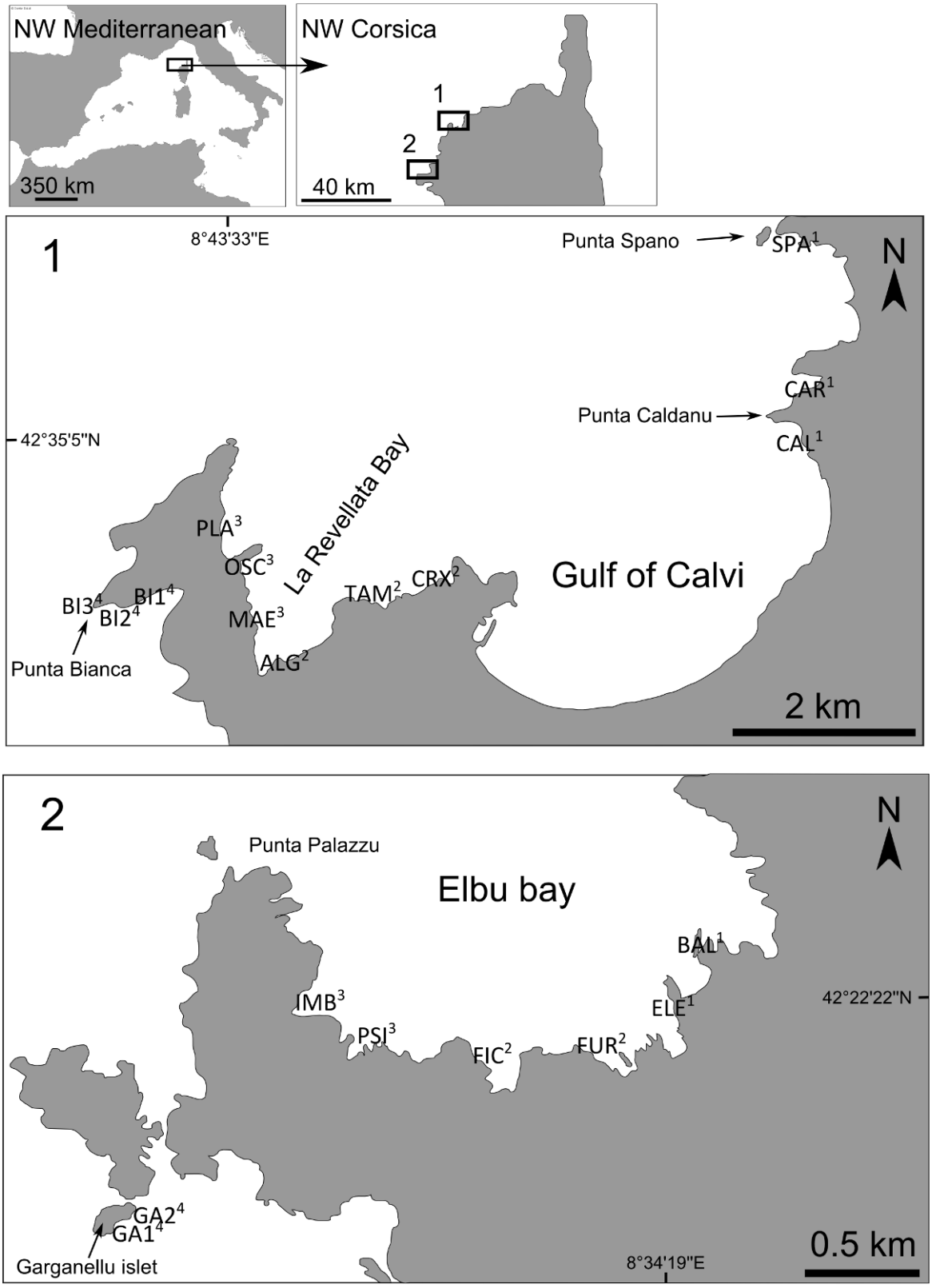

Fig. 2. For each studied localities (1 and 2) study sites are indicated in capital letters – superscript arabic numbers indicate repartition of site by zones – 1: La Revellata bay and Calvi Gulf; 2: Elbu bay in the Scandola Natural Reserve

3.3.1 Data treatment and preliminary results

3.3.1.1 Methodological calibration

As a first result, the obtained data set allowed me to validate the fish juvenile census methodology used, by verifying its accuracy in our 20 sites (Fig. 3 on next page): for each of these sites (Fig. 2), within the *Cystoseira* forest habitat, I plotted (Fig. 3) the cumulated mean abundance per square meter for *Symphodus* spp. (i.e. including *S. roissali*, S*. ocellatus*, *S. tinca*) according to the number of census replicates (one replicate = one census of 5 min within 1 m², Fig. 4). In 2/3 of sites, cumulated mean abundance tended to stabilize after performing about 7 census replicates (Fig. 3). As a conclusion, we decided to perform at least seven 1m² replicates of juvenile census for a given site of *Cystoseira* forest.

However, for future studies I would recommend if possible to increase it up to 10 replicates more particularly if one wishes to detect small variations of fish juvenile densities, e.g. when studying *Symphodus* spp. juvenile densities according to depth in a given habitat (see ongoing collaborative studies in perspectives in Chapter VI).

Fig. 4. Underwater visual census of juvenile fishes, on a *C. balearica* forest. Elbu Bay (ELE site), 6th of August 2010 , depth = 3.0 meters (photo: O. Bianchimani)

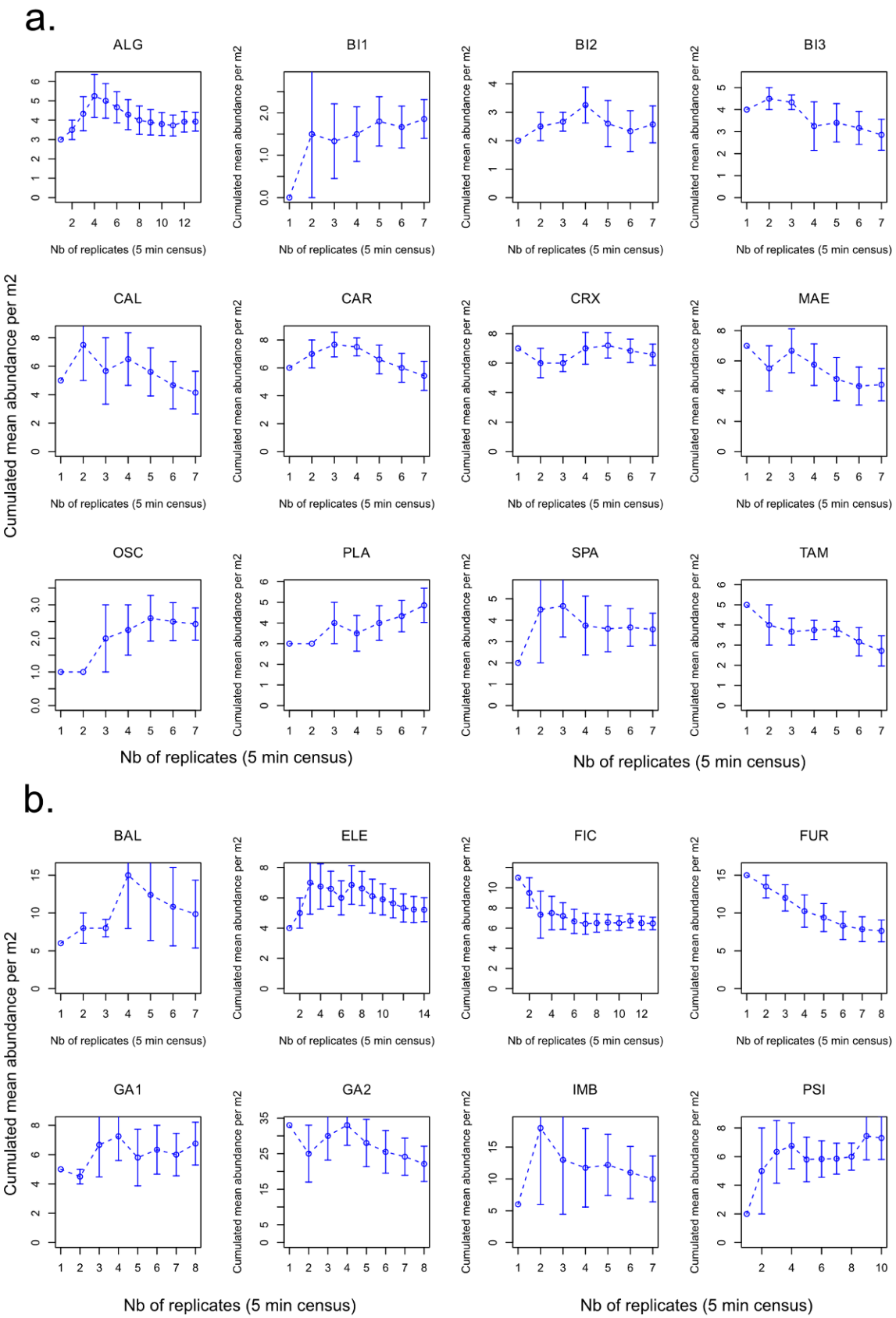

Fig. 3. Cumulated mean abundance per square meter for *Symphodus* spp. for sites in La Revellata (a) and Scandola (b) (see Fig. 2 for sites localization)

*3.3.1.2 Abundance patterns across habitats (*Cystoseira *forests* vs. *Dictyotales-Sphacelariales bushland)*

A model was fit to juvenile assemblage densities in order to test its response to habitats, localities, zones and sites: factor habitat has two levels (*Cystoseira balearica* and DS) and is fixed, factor locality has two levels (Revellata and Scandola) and is random, factor zone has 4 levels (Z1 to Z4 in both localities, see Fig. 2), is random and nested in Factor locality, factor sites has 12 levels in La Revellata (SPA, CAR, CAL, CRX, TAM, ALG, MAE, OSC, PLA, BI1, BI2, BI3) and 8 levels in Scandola (BAL, ELE, FUR, FIC, PSI, IMB, GA1 and GA2), is random and nested in factor zone. The same model was applied to taxa-specific densities. In order to compare densities between levels of factors we performed for the assemblage a PERMANOVA (PERmutational Multivariate ANalysis Of VAriance) and for taxa-specific densities a PERANOVA (PERmutational univariate ANalysis Of Variance) (Anderson, 2001) on the model including terms and all interactions (Underwood, 1981) and terms were then pooled as suggested by Anderson et al. (2008). Analysis were based on the binomial deviance (scaled) dissimilarity measure (Anderson and Millar, 2004). P-values were obtained by 9999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200).

Juvenile assemblage differed according to habitat (PERMANOVA, F = 7.93, P = 0.064) and this difference was consistent through space since interaction terms between habitat and locality and between habitat and site were not significant (Fig. 5b, PERMANOVA, respectively F = 1.49, P = 0.288 and F = 1.29, P = 0.177). On one hand juvenile assemblages in *C. balearica* forest were mainly associated with high densities of *Symphodus* spp. and (to a lower extent) high densities of *Labrus* spp. and on the other hand with rather low densities of *Coris julis* and Blenniidae-Gobiidae-Tripterygiidae (crypto-benthic taxa); inversely, DS bushland juvenile assemblages were associated with high densities of *C. julis* and crypto-benthic taxa and relatively low densities of *Symphodus* spp. (Fig. 5a and Fig. 5b).

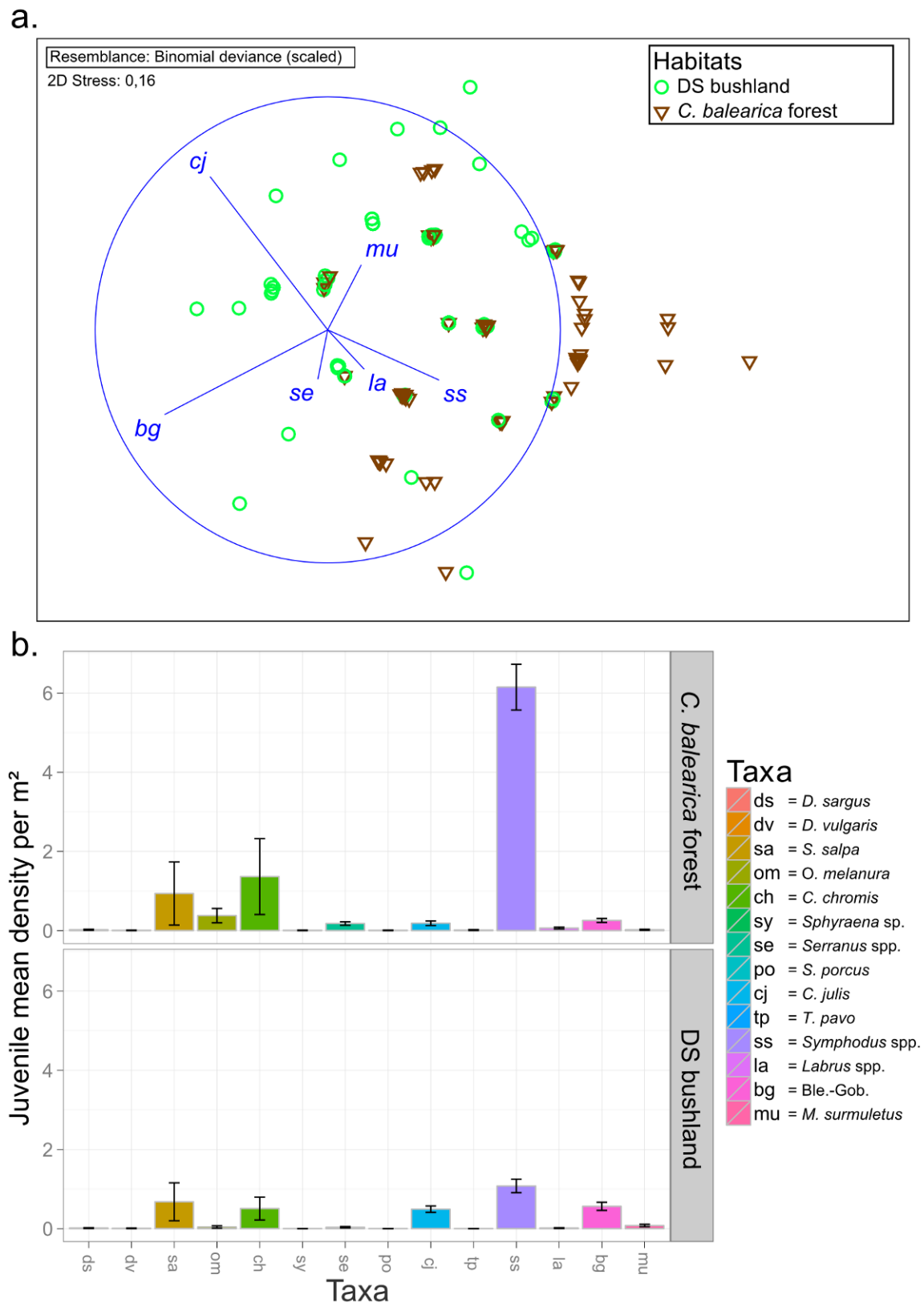

Fig. 5. Juvenile assemblage in both studied habitats; a: nMDS ordination plot of samples with taxa densities correlation vectors (Spearman) ; only vectors with correlation >0.2 are plotted (see Chapter IV-2 for a detailed M&M on nMDS); b: the mean juvenile assemblage in *C. balearica* forest differed significantly from the mean one observed on Dictyotales-Sphacelariales bushland (PERMANOVA, F = 7.93, P = 0.064); error bares = SE

When looking at taxa-specific density, for *Symphodus* spp. (the most abundant taxa in studied habitats, see Fig. 5b), interaction term between habitat and locality was significant (PERANOVA, $F = 12.03$, $p = 0.008$) and therefore I performed new analysis separately for each locality. Both in La Revellata and Scandola, habitat term was significant (PERANOVAs, respectively $F = 128.58$, $p = 0.028$ and $F = 25.64$, $p = 0.030$): *Symphodus* spp. densities were higher in *C. balearica* forest than in DS bushland (Fig. 6a); in La Revellata this pattern was consistent through all sites : interaction term between habitat and site was not significant (PERANOVA, $F = 1.42$, $p = 0.199$) and although densities varied in a given habitat (Fig. 6b) the abundance pattern across habitats was similar; in Scandola this interaction term was significant ($F = 5.78$, $p < 0.001$) but there again *Symphodus* spp. densities were systematically higher in *Cystoseira* forest than in DS bushland and this significant interaction was probably due to one site (GA2) were densities of *Symphodus* in the forest were about one order of magnitude higher than in other sites (Fig. 6b).

Therefore, in both locality abundance patterns observed in the previous part (2009) for *Symphodus* spp. juveniles (i.e. [*C. balearica*] > [DS bushland]) was consistent through time (2009 and 2010 for "ELE" site) and space (20 Corsican sites in 2010).

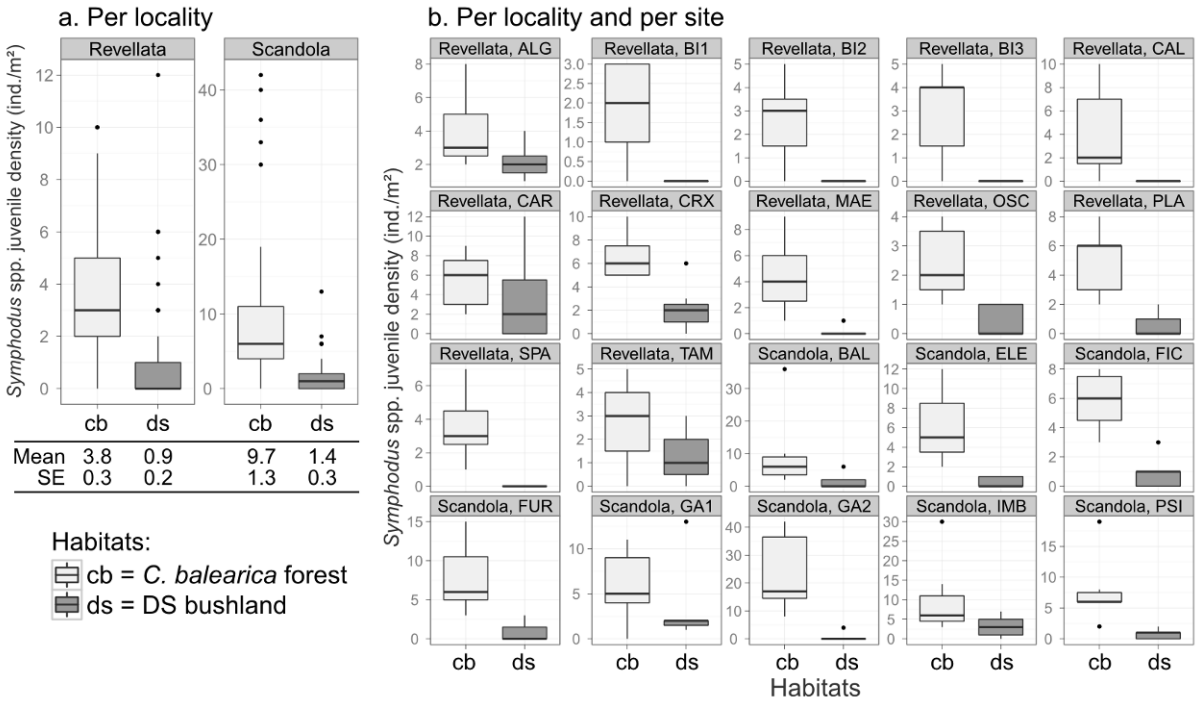

Fig. 6. Tuckey boxplots of *Symphodus* spp. densities within both studied habitats - a: habitat term for both locality (see PERANOVAs results in the text); mean and standard error (SE) are given – b: habitat term for each site per locality (see sites localization on Fig. 2)

3.3.1.3 Spatial variability of fish juvenile assemblage within Cystoseira *forests:* preliminary results

Studying *C. balearica* alone, a similar model as previously was fit to assemblage and taxa-specific densities in order to test its response to locality, zones and sites (same levels). For the full juvenile assemblage of *C. balearica* forests, locality, zones and sites terms were significant (Table 1). The estimates of components of variation indicated that the "zone", "locality" and "site" term explained respectively 10.5, 9.7 and 5.9 % of the variability.

Table 1. PERMANOVA table of results: juvenile assemblage

Source of variation	df	MS	Pseudo-F	P (perm)	
Locality (lo)	1	7.29	3.24	0.0591	·
Zone zo(lo)	6	2.31	2.60	0.0098	**
Site si(zo(lo))	12	0.89	1.56	0.0392	*
Residuals	120	0.57			
Total	139				

ns: not significant · $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$
P-values were obtained by 9999 permutations of residuals under a reduced model

For *Symphodus* spp., locality and sites terms were significant (Table 2). The estimates of components of variation indicated that the "locality" (Revellata and Scandola) and "site" (12 and 8 sites) term explained respectively 28.6 and 21.1 % of the total variability.

Table 2. PERANOVA table of results: *Symphodus* spp. juveniles

Source of variation	df	MS	Pseudo-F	P (perm)	
Locality (lo)	1	1173.90	11.28	0.0084	**
Zone zo(lo)	6	103.76	0.94	0.5243	ns
Site si(zo(lo))	12	110.55	3.90	0.0001	***
Residuals	120	28.32			
Total	139				

ns: not significant · $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$
P-values were obtained by 9999 permutations of residuals under a reduced model

Consequently, since locality term was significant it was adequate to perform further analysis separately for each of the two localities. In La Revellata (Fig. 7a), juvenile assemblages within *Cystoseira* forests varied in space so that we can distinguish forests mainly characterized by a higher coverage of *Cystoseira*, shallower depth and which displayed higher densities of *Symphodus* and *Oblada melanura.* Inversely deeper forests tended to be characterized by sparser cover of *Cystoseira* and displaying higher densities of Blennidae-Gobidae, *Coris julis*, *Chromis chromis* and *Serranus* spp. In Scandola (Fig. 7b), juvenile assemblages varied among samples with a strong correlation with *Serranus* spp. and *Coris julis* juvenile densities: samples showing higher *Serranus* densities belonged more particularly to sites displaying

fractured substratum (pers. obs.) and *Serranus* densities might therefore be partly explained by availability of habitats (including crevices) for this taxa. Samples displaying higher densities of *C. julis* juveniles were those characterized by lower height and percent-cover of *Cystoseira* and corollary higher cover of DS assemblage (Fig. 7b); this confirmed our previous results (part 3.2). *Cystoseira* forest samples showing the highest *Cystoseira* canopy height and cover tended to be associated with juvenile assemblage displaying high densities of *Labrus* spp., *Symphodus* spp. and *Oblada melanura* (Fig. 7b).

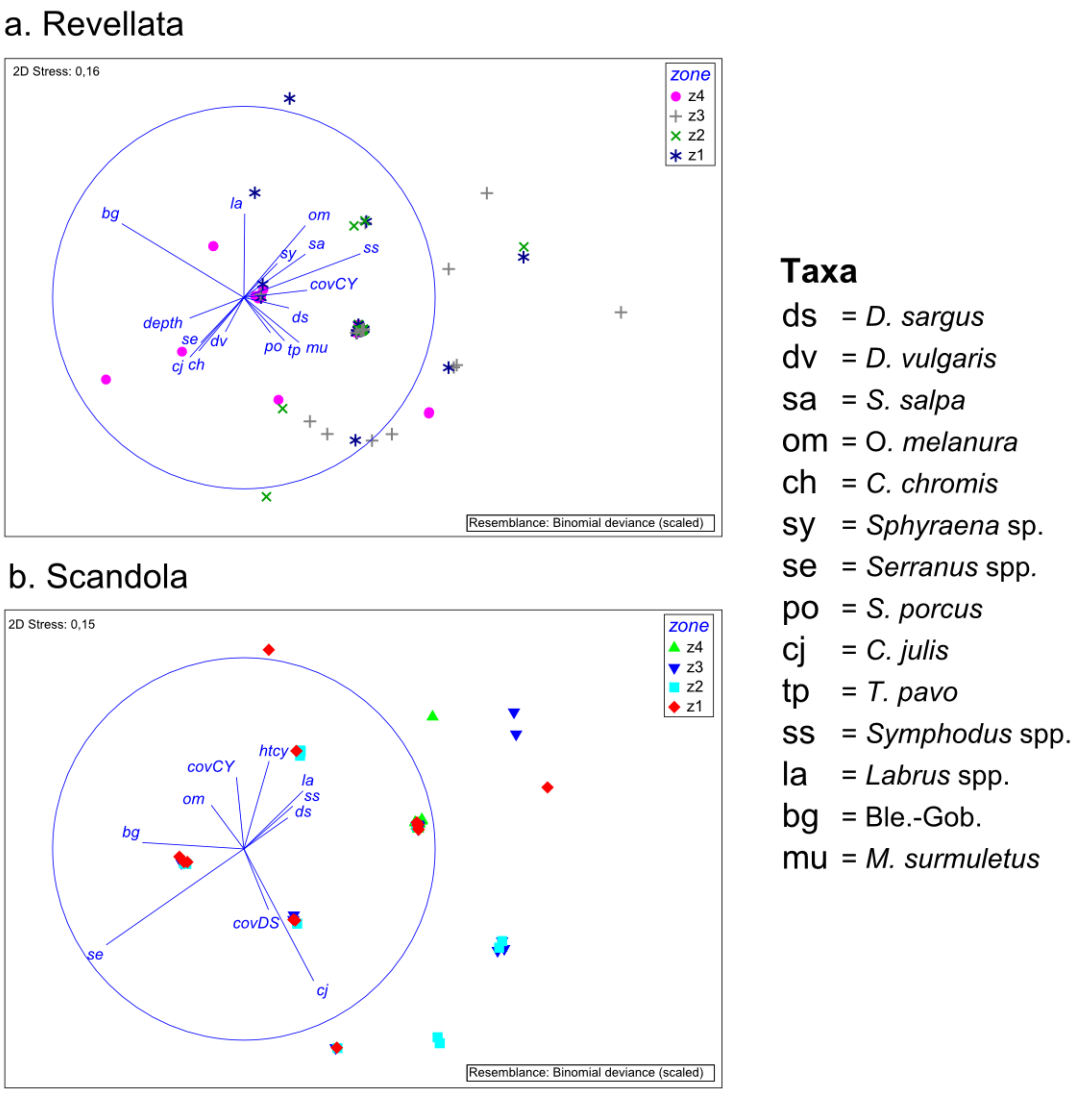

Fig. 7. nMDS ordination plot of fish juvenile assemblages within *C. balearica* forests for both localities. Only correlation vectors (Spearman) with correlation >0.2 are plotted (see Chapter IV-2 for a detailed M&M on nMDS) – abiotic and biotic features: *Cystoseira* percent cover (covCY) and canopy height (htcy), DS percent cover (covDS) and depth. Zones: see Fig. 2.

As a conclusion, abundance patterns observed in 2009 were confirmed in 2010 and were consistent through space at scales of 1, 10 and 20 km: *Symphodus* spp. juveniles were mostly associated to *Cystoseira balearica* forests rather than to DS bushland, *C. julis* juveniles were associated to Dictyotales-Sphacelariales bushland or *Cystoseira* forests with some mixed cover of Dictyotales-Sphacelariales, and for *Serranus* spp. juveniles spatial variability could not be explained by macrophyte assemblage features and may therefore depend on other micro-habitat characteristics. We saw that part of the spatial variability of juvenile densities for a given habitat (*Cystoseira* forests) was correlated to habitat abiotic and biotic features (notably small-variations in depth and canopy height). Data will be explored more deeply taking this into account in the article in preparation; notably through the use of DISTLM routines (Clarke and Gorley, 2006) allowing to identify co-variables that must be integrated in a PERMANOVA design (Anderson et al., 2008) before checking if some residual spatial variability is still observed. Such a residual spatial variability in taxa-specific juvenile densities for a given habitat would subsequently be attributed to other factors, such as larval and settler supply by oceanographic currents.

3.4 Supplementary data: Nursery value of two canopy forming habitats, Cystoseira forests versus Posidonia oceanica *meadows*

In two sites (ALG and MAE, see Fig. 2 of part 3.3) within Revellata Bay, a pilote study was performed in order to compare the juvenile assemblage specific composition and densities in the three main macrophyte-formed habitats of the bay: *C. balearica* forest and DS bushland were compared to a third habitat, *Posidonia oceanica* meadows. Within the two sites, two divers (A. Cheminée and J. Pastor) performed juvenile fish underwater visual counts using the same methodology as previously described, within 11 random replicates of each of the three macrophyte-formed habitats. Depth (between 1 and 4 meters), substratum and slope (gentle to pronounced flat rocky stands) were kept as much as possible constant. In each 1 m² replicate canopy height and percent cover of the dominant assemblages were measured (n = 8) (Fig. 8a).

For the most frequent taxa observed in these sites (*Symphodus* spp., *Sarpa salpa* and *Chromis chromis*), *C. balearica* forest displayed higher densities of juveniles than the *P. oceanica* meadow (Fig. 8). A different, opposed pattern has been observed in Menorca, Balearic islands (A. Cuadros-Casado, pers. com.): *Symphodus* spp. juveniles were observed mostly in *P. oceanica* meadows rather than in the neighboring *C. balearica* forest, in sites where the *Cystoseira* canopy was very low (<8 cm canopy height, about 80% percent cover). We may interpret the opposed patterns observed as a shift of juveniles toward the most complex habitat offering better refuges against predators: in sites where the *Cystoseira* canopy is sparse or low, other macrophyte-formed habitats might be preferred by juveniles due to a higher quality in terms of food availability and predation risk (Hindell et al., 2000). These processes are further discussed in the next part (Chapter III-part 5).

Nevertheless, my preliminary data from La Revellata Bay may be biased by the methodology used: five-minutes counts within 1 square meter may not be fitted to *P. oceanica* meadows, where detectability of juveniles may significantly be different than in *Cystoseira* forests (Francour, 1999; Harmelin-Vivien et al., 1985), notably due to the significantly different tri-dimensional structure characteristics (leaf or thalli height) of these erect macrophytes (Fig. 8, a). Consequently no conclusion can be inferred from these preliminary data and further research is needed to compare the nursery value of various macrophyte-formed habitat of the Mediterranean infralittoral seascapes (see Chapter VI, perspectives).

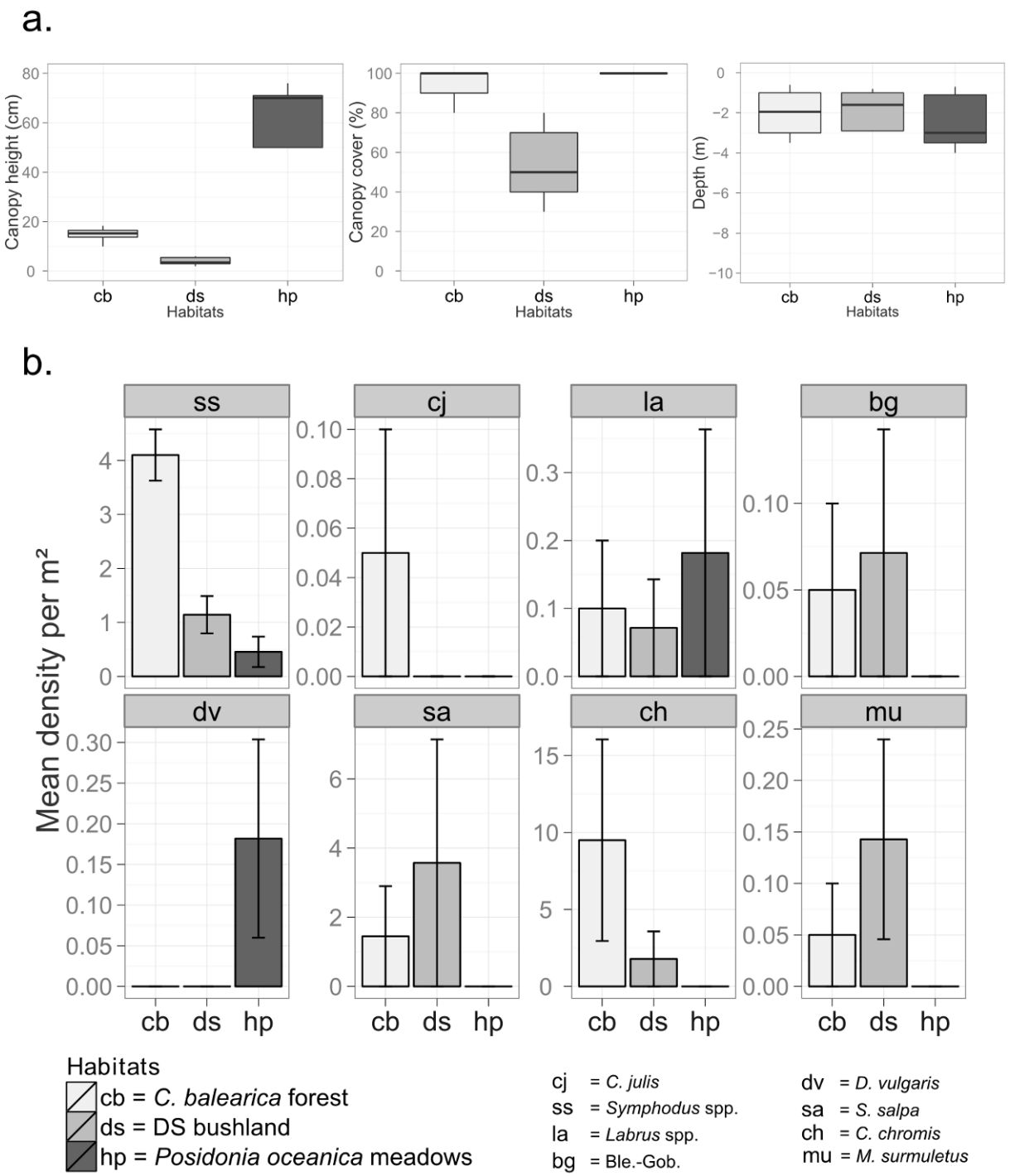

Fig. 8. a: Tuckey boxplots of dominant assemblage (cb, ds or hp) canopy height and percent cover, and depth in each studied habitats; b: Juvenile mean densities (error bare = SE) in each studied habitats.

3.5 Which may be the underlying processes explaining macrophyte-formed habitats nursery value?

3.5.1 Introduction

In the previous parts we highlighted the high nursery value –*sensu* Beck et al. (2001)- of *Cystoseira* forests notably for some abundant Labridae species. In this part, the underlying processes driving such abundance patterns are addressed. Part 3.5.2 is a contribution to the Springer-Verlag published proceedings of a congress held at Brest (France) in March 2011: "Séminaire scientifique et technique sur les paysages sous-marins". After giving some more examples of macrophyte-formed habitats nursery role, it draws a mini-review of the classes of ecological processes potentially driving juveniles' abundance patterns: (i) differential settlement/recruitment, (ii) differential mortality and (iii) active choice of the favored habitat. Part 3.5.3 gives the abstract of a Master student thesis I co-supervised which addressed more particularly the two last classes of processes through an *ex-situ* approach and part 3.5.4 gives some *in-situ* supplementary observations I made as illustrations.

3.5.2 Nursery role of macrophyte-formed habitats: abundance patterns and underlying processes under a seascape approach

Thiriet, Cheminée and Francour (accepted)

Nursery role of macrophytes-formed habitats: abundance patterns and underlying processes under a seascape approach

Accepted for the proceedings of "Séminaire scientifique et technique sur les paysages sous-marins" – Brest (France), 29 - 31 of March 2011; to be published by Springer-Verlag.

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Macrophytes: threatened habitat formers among the seascape mosaic

Infralittoral seascapes are made of a mosaic of various habitats (Grober-Dunsmore et al., 2009), including macrophyte (i.e. macroalgae and seagrass) formed habitats. Indeed, macrophytes are biological formers of habitat complexity at a spatial scale from 10^{-1} to 10^{2} m. Furthermore, one taxon may dominate the macrophyte community according to its own architectural complexity (i.e. tri-dimensional structure, e.g. degree of branching) and density, and thus modify the habitat in such a manner that it is considered as a fully-fledged habitat (e.g. the Cystoseiretum described by Verlaque (1987)). Moreover it is acknowledge that macrophyte-formed habitats are characterized by the presence of a canopy (Dayton, 1985).

It has been reported worldwide that infralittoral habitats are subject to strong regression due to anthropogenic pressures (Coll et al., 2010): for example, in the case of macrophytes-formed habitats, the Mediterranean *Cystoseira* (Phaeophycea) forests (Mangialajo et al., 2007; Sala et al., 2011; Thibaut et al., 2005) and *Posidonia* seagrass meadows (Francour et al., 1999; Guidetti and Fabiano, 2000) have been reported to regress due e.g. to water pollution, coastal urbanization, boat anchoring, or invasive species (Claudet and Fraschetti, 2010).

Nursery role of macrophytes

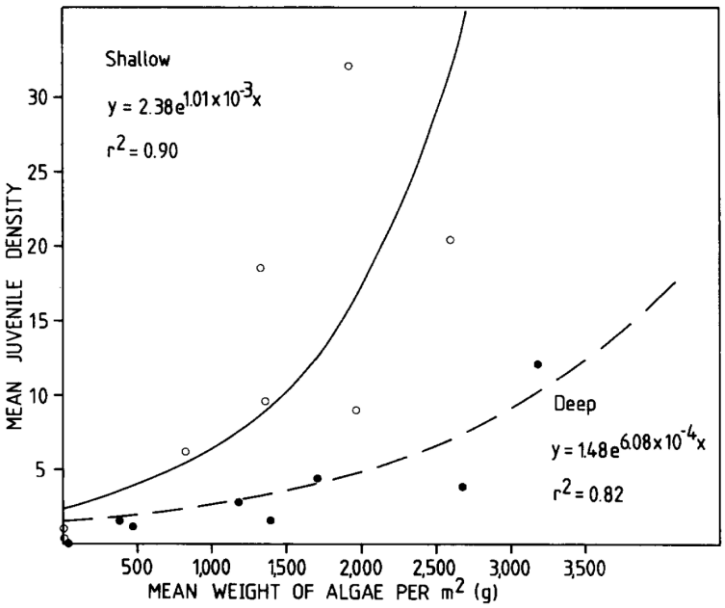
Many studies carried out worldwide in temperate coastal marine areas report that fish assemblages usually exhibit different patterns of composition and abundances between habitats. Focusing on post-settlement juveniles (hereafter called 'juveniles'), for a given fish species or set of fish taxa, some habitats exhibit on average higher densities than others. They have therefore a higher nursery value for the considered fish taxa, for which they consequently play a nursery role (Beck et al., 2001). Worldwide studies compared the

nursery value of habitats among infralittoral seascapes and highlighted the nursery role of canopy-forming macrophyte habitats. Examples include *Ecklonia* and *Carpophyllum* (Phaeophycea) forests of temperate rocky reefs of New Zealand (see Box 1 (Jones, 1984)), *Cystoseira* forests of temperate rocky reefs of the Mediterranean (see Box 2; (Cheminée et al., under review)) and the Mediterranean temperate *Posidonia oceanica* seagrass meadows (Box 3; (Guidetti, 2000)).

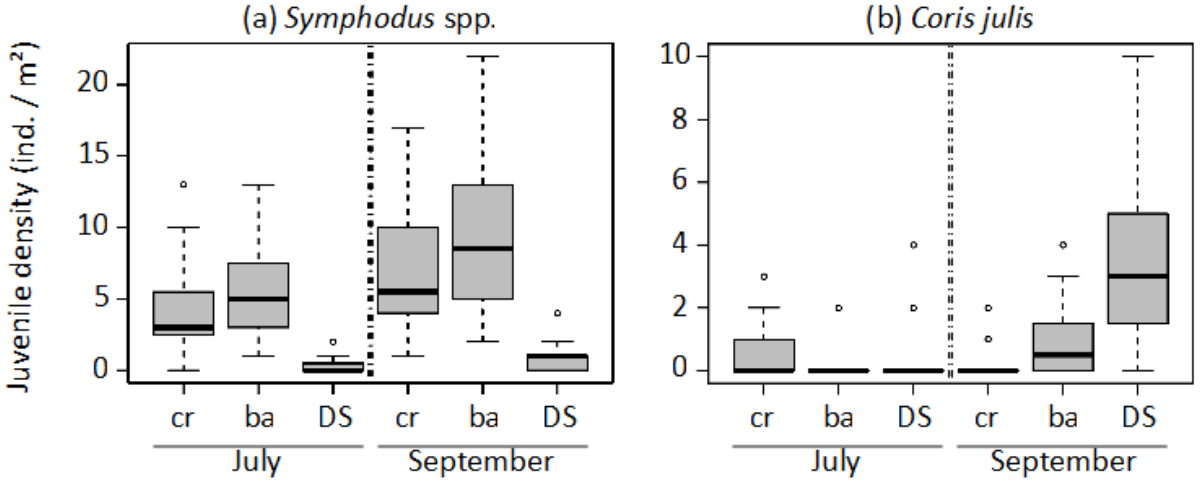
According to their regression and given the functional importance of such canopy-forming habitats through their nursery role, these habitats must be taken into account when analyzing the global seascape for conservation and management perspectives. Indeed, protecting the juvenile habitats may be one of the most effective fisheries management measures (van de Wolfshaar et al., 2011).

Box 1: An example of a study higlighting the nursery role of a kelp forest among various temperate rocky reef habitats of New Zealand – from Jones (1984)

In NE New Zealand, within the habitat composed by the canopy forming Phaeophyceae *Ecklonia* and *Carpophyllum*, Jones (1984) showed that mean juvenile densities (*Pseudolabrus celidotus*, Labridae) increased exponentially with the mean weight of algae per square meter. This significant effect was even stronger in shallow (<8m) than in deeper (>8m) areas (see graph). Besides, in the same study, a macro-algal removal experiment resulted in significantly lower juvenile fish recruitment (59.6 ± 10.0 *versus* 10.2 ± 2.3 (mean + se) juveniles per 25 m² respectively in the control area *vs* in the cleared area). It was confirmed by an increased recruitment (18.8 ± 3.3 (se) juveniles per 500 m²) observed after the recovery of an algal forest over a previously barren rocky reef (3.2 ± 0.9 (se) juveniles per 500 m² in an equivalent barren control area).



Box 2: An example of a study higlighting the nursery role of Meditteranean *Cystoseira* forests - from Cheminée et al. (under review)



In 2009, Cheminée et al. (under review) studied the nursery value of the biocenosis of photophilic macrophytes of the Mediterranean rocky infralittoral biotope, including the canopy forming *Cystoseira* (Phaeophyceae, Fucales) forest and its alternate stable states created by anthropogenic or natural disturbances. Juvenile fish densities of several taxa and more particularly of *Symphodus* spp. (see left box plot) were consistently through time significantly greater in the two *Cystoseira* forests ('cr' and 'ba') than in the less complex bushy assemblages of Dictyotales and Sphacelariales (DS). Moreover, experimental habitat manipulation mimicking an alteration of a *Cystoseira* canopy (e.g. using artificial plastic thalli) showed significantly greater abundances of *Symphodus* spp. juveniles on artificially forested substratum than on bare substratum, highlighting the importance of the presence of a canopy. However contrasted responses may be found for other fish species: in September (see right box plot) *Coris julis* densities were significantly higher in the bushy Dictyotales-Sphacelariales facies than in both *Cystoseira* facies.

This study quantified for the first time the functional importance of the *Cystoseira* forest canopy, and suggested that these habitats act complementarily with other key habitats of infralittoral seascapes and that their loss may strongly affect the replenishment of littoral fishes at the upper seascape scale.

Box 3: An example of a study higlighting the nursery role of Mediterranean *Posidonia oceanica* seagrass meadows – from Guidetti (2000)

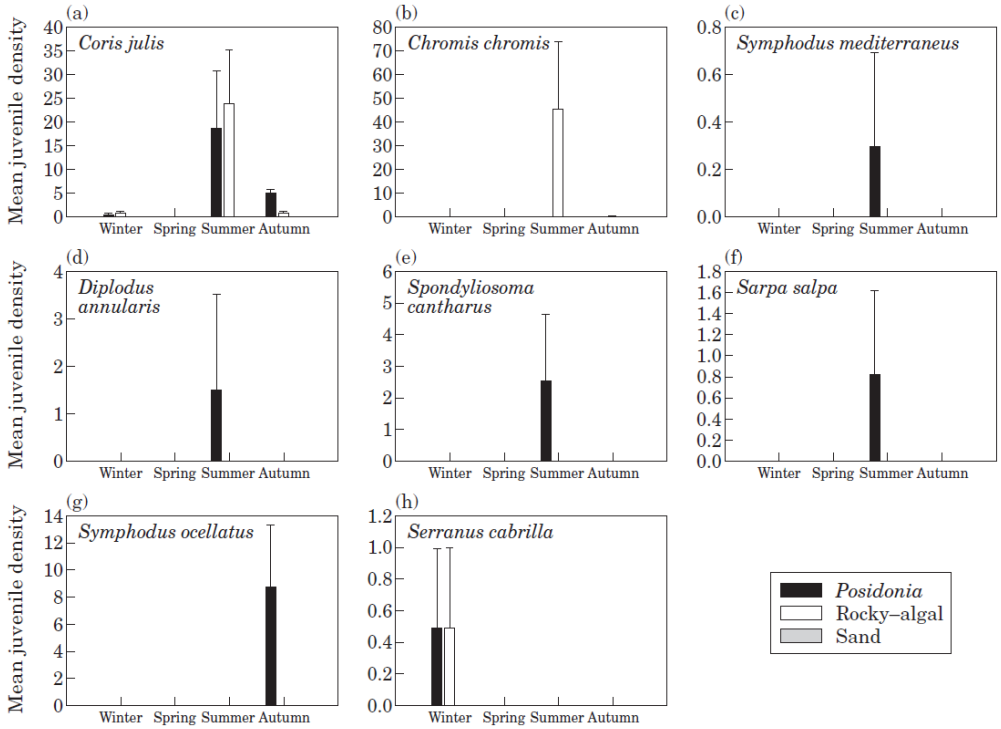


FIGURE 8. Mean density (mean number of individuals of juveniles 40 m^{-2}) of common fish species. Bars indicate standard deviations.

Guidetti (2000) highlighted the nursery role of the canopy forming *Posidonia* meadows: juveniles of *Symphodus ocellatus*, *Symphodus mediterraneus*, *Serranus cabrilla*, *Diplodus annularis*, *Spondyliosoma cantharus* and *Sarpa salpa* were significantly more abundant over *Posidonia oceanica* meadows (in black, see histograms) than over rocky-algal or sand habitats, while juveniles of *Chromis chromis* inhabited predominantly rocky-algal bottoms. Small individuals of *Coris julis* were censused over both *P. oceanica* and rocky-algal habitats. Contrastingly, bare sand did not host any juveniles among these species. The author suggested that differences in fish species richness and abundance are primarily related to habitat structure, e.g. the tri-dimensional structure of the canopy forming *Posidonia* meadows.

Three classes of ecological processes potentially drive abundance patterns

Worldwide in temperate coastal waters, densities of post-settlement juveniles are for many taxa higher in macrophyte-formed habitats than in less structured habitat such as bare substrate (see section above). Evolutionary processes selected functional and behavioral traits that are adapted to specific environments. The pool of functional and behavioral traits is filtered by environments through ecological processes what governs distribution patterns of species among habitats (Morris, 2011). Ecological processes may be studied according to three broad classes: (i) differential settlement/recruitment, (ii) differential mortality and (iii) active choice of the favored habitat. None of them is necessary exclusive and differences in composition and abundance of species between habitats could be the result of their combination (Morris, 2003; 2011; Olabarria et al., 2002a).

Differential settlement acts at a wider spatial scale than habitats distribution

Most of demersal fish species inhabiting temperate coastal waters worldwide experience a complex life cycle. Usually, it is divided into a vagrant planktonic phase (corresponding to the stages egg and larvae) and a relatively sedentary benthic phase (from the stage post-settlers to adult) (Di Franco et al., 2011). During the planktonic phase, eggs and larvae disperse depending mainly on oceanographic patterns. The metamorphosis from larvae to juvenile triggers the transition from planktonic to benthic environment, a process called "settlement". Due to oceanographic patterns (such as currents), juveniles that passively dispersed may settle in greater number in one locality than to others (Di Franco et al., 2011).

In coastal environments, seascapes are usually heterogeneous at a fine spatial scale, and the different habitats are interspersed forming a mosaic-like structure. Considering that difference in larval arrival occurs at a spatial scale that encompass habitat heterogeneity, all habitats composing one locality homogenous in terms of larval arrival will exhibit the same settlement rate. According to this point, local differences in post-settlement juveniles between adjacent habitats should be due to differential mortality or movement across habitats rather than difference in larval supply. This however stresses the need to consider multiple spatial scales when studying links between habitat and post-settlement juveniles (Rilov and Schiel, 2011).

Differential mortality and active habitat selection are both mediated by differential habitat quality

At a fine spatial scale, assuming that different habitats have been exposed to the same settlement rates, difference in post-settlement juveniles' densities among habitats may be due to differential mortality and/or active choice of the favored habitat. Considering that this active choice is a behavior that appeared as a result of natural selection, the chosen

habitat shall be the one where the individuals have the highest probability of growing and surviving until reproduction (Morris, 2011). Therefore, the two classes of processes, differential mortality and active habitat selection, are both mediated by differential habitat quality in terms of food availability and predation rate (Hindell et al., 2000). The highest quality habitat minimize mortality rate by offering the trade-off between foraging and safety (Anholt and Werner, 1998; Dahlgren and Eggleston, 2000).

Habitat quality is affected by structural complexity of macrophyte-formed habitat:

The case of food availability

Food supply is one of the basic needs for any heterotrophic organism. Food gives the caloric energy, nutrients and vitamin needed to keep body-functioning, growth and development, and reproductive potential. Individuals experiencing starvation lose fat and muscle mass (decrease in condition) in order to keep vital systems. Growth and development of juveniles may be altered (Heck et al., 2003) as well reproductive potential of adults (Ordines et al., 2009). Energy deficiency reduces physical abilities and ultimately results in death. Low food availability may therefore causes direct mortality of post-settlement juveniles or indirect mortality through (a) a reduction of size-at-age making longer the period of vulnerability toward size-selective predation ("the bigger is better" hypothesis, (Levin et al., 1997; Sogard, 1997), and (b) a reduction of their physical abilities to escape predator attack (Levin et al., 1997).

Availability of food resources depends on their quantity and their accessibility. Macrophytes affect both of them. Plants architecture (e.g. degree of branching) and densities affect the structure of benthic macroinvertebrate assemblages. In several regions worldwide, habitats made up of structurally complex macrophytes harbor higher diversity and abundances of macroinvertebrates (Chemello and Milazzo, 2002; Christie et al., 2009; Hansen et al., 2010; Parker et al., 2001). These habitats may therefore be particularly suitable as feeding grounds for invertebrate feeders such as many demersal fishes. However, it has been suggested that extremely high structural complexity may alter fishes' foraging efficiency through physical constraint (Heck and Orth, 1980; Stoner, 1982). Another characteristic potentially affecting invertebrate accessibility is the rigidity of macrophytes. A very flexible canopy is more sensitive to water movement and its constantly moving back-and-forth, what may limit access for fishes to understory invertebrates (Levi, 2004).

The case of predation rate

In several regions worldwide, post-settlement juveniles are known to be prey item for various predators. Predation mortality may therefore drive differences in abundance patterns of juveniles between habitats (Beck et al., 2001; Heck et al., 2003; Hindell et al.,

2000). Analyzing and quantifying interactions between predator, prey and environmental factors is a quite complex task. For this purpose, the act of predation may be broken into a series of sequential stages which are studied separately : prey detection and location by the predator, pursuit and attack, and capture (O'Brien, 1979).

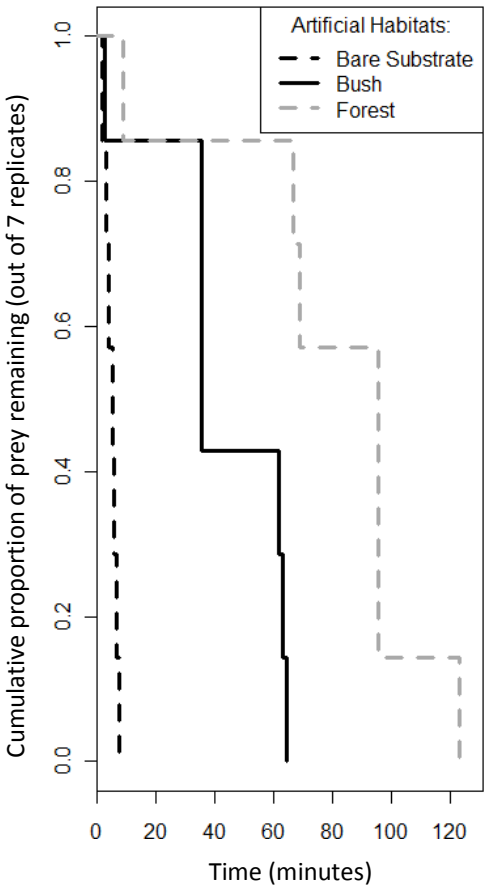
The predation act may be accomplished according to three different tactics. The chase (or pursuit) predator actively searches a prey item and uses its superiority in swimming speed for catching. In opposition, the sit-and-wait (or ambush) predator counts rather on the surprise. It waits motionless camouflaged in the environment until one prey enters its attack range (small). An intermediate tactic is used by the stalk-attack predator. It actively searches for prey item. Once a prey detected, it approaches furtively until the prey is within attack range (medium) and makes a speed burst to capture (Horinouchi et al., 2009a; Matsuda et al., 1993; Schultz and Kruschel, 2010).

Habitat structural complexity interacts with different stage of the predation act, affecting predation success differently depending on the tactic. In highly complex habitat, habitat-elements may interfere with prey detection/location for active searcher (chase and stalk-attack tactics), while for ambush predator, encounter rate depends only on prey density and mobility. Moreover, mobility of predators (that are most of the time larger than their prey) may be relatively more constrained by habitat-elements than prey mobility. This sharply decreases chances of success for chase predator (long distance pursuit) and slightly for stalk-attack predator (medium distance pursuit). Because ambush tactic involve almost any predator mobility, habitat structural complexity should not facilitate prey escape. In some way, it may also be considered that habitat-elements enhance furtive wait of ambush predator and furtive approach of stalk-attack predator, for both tactics the use of camouflage is of paramount (see Box 4) (Lima, 1992; 1998; Lima and Dill, 1990).

From these considerations, the chase tactic does not seem to be suitable in highly complex habitat while ambush tactic does. It is less clear-cut for stalk-attack tactic. Some predators are able to use only one tactic (specialist) while some others are able to use several tactics (generalists) depending on the environment. The relation between habitat and predation tactic suitability is probably a strong driver of distribution patterns of specialist predators among habitats (habitat-specific predators) (Schultz et al., 2009). Dealing with this, predation mortality of juveniles in a given habitat depends on their ability to escape associated predator (by different strategies such as particular microhabitat use) (see Box 5). Thus, in general, coevolution between habitat-specific predator and prey juveniles results in specialized escape strategies (1990; Lima, 1992). This specialization in escape strategy would lead the prey to better survive in - and/or to choose - the habitat of its coevolved predator rather than another habitats where it has less ability to escape from predators practicing other tactics (Lima, 1992).

Box 4: An example of experiment evidencing the interaction between predation success and habitat architectural complexity - from Thiriet et al. (in prep)

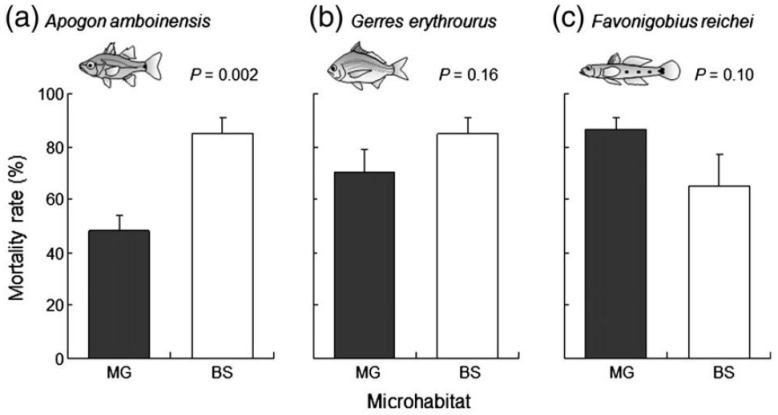
Thiriet et al. (in prep.) studied interaction between predation efficiency and habitat architectural complexity. To avoid confounding effects with food availability, experiments were done in tanks. Artificial habitats of increasing architectural complexity were constructed using different densities and lengths of plastic algae: Bare Substrate, Bush (sparse and short stems), Forest (dense and long stems). The biological models were two co-occurring demersal fishes in Mediterranean Infralittoral rocky reef: the piscivorous *Serranus cabrilla* preying on the post-settlement juvenile *Symphodus ocellatus*. Survival of one prey facing one predator was assessed in the three habitats on seven occasions (replicates). Survival curves (see figure) were compared between habitats using the Mantel-Haenszel test. On average, survival time in Forest was 1.9- and 16.5-fold greater (significantly) than respectively in Bush and Bare Substrate. These results clearly evidence that high habitat architectural complexity may reduce efficiency of one predator. This does not necessarily mean that predation mortality of juveniles is reduced too because of natural densities of predators which potentially differ between habitats.



Survival curves in the 3 artificial habitats

Box 5: An example of a study comparing predation mortality of juveniles between habitats using tethering experiments - from Nanjo et al. (2011)

In order to compare predation mortality of juveniles between habitats, tethering experiments are adequate since they take into account both the efficiency of the predator (habitat and predation-tactic dependent, see previous box) and the density of the predator in a given habitat. Nanjo et al. (2011) studied predation rates on juveniles of three fish species using tethering experiment. For the resident, necto-benthic *Apogon amboinensis*, the predation mortality was significantly lower in "vegetated" habitat (mangrove root area) than in "unvegetated" habitat (bare sand area) (see (a) in boxplots), although predatory fish were more present in the vegetated habitat. No differences in mortality rates were found for two other species: the active swimmer *Gerres erythrourus* (b) and the crypto-benthic *Favonigobius reichei* (c). These mortality rates may be explained by contrasting anti-predator tactics, either associated with mangrove structural complexity offering shelter (in the case of *A. amboinensis*) or independent of mangrove vegetation structure (for the two other species).



Interactions between adjacent habitats: the putative edge effects

Previous sections report that each habitat composing the seascape has its own functioning (mediated in part by its structural complexity) what results in differential abundance patterns. However, at the boundary between two habitats (i.e. ecotone), their respective functioning affect each other and particular abundance patterns may appear in this transition area (usually higher diversity and abundance than both sides added), this phenomena is called edge effect. Global increase in habitat fragmentation and its propensity to increase the amount of ecotone and consequently edge effects (Smith, 2010) stresses the need to better understand underlying mechanisms.

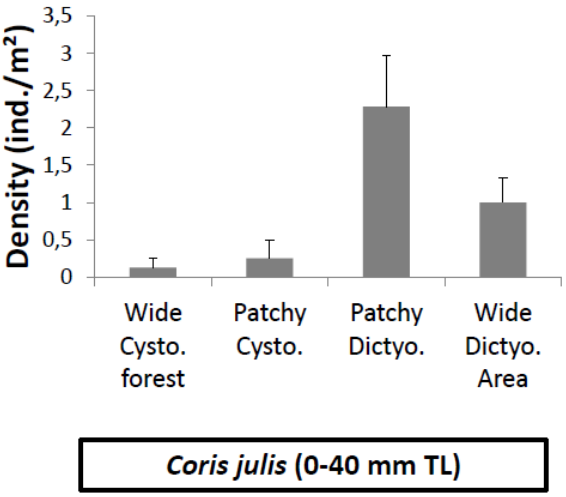
Edge effect may come from emergent physical properties. For instance, at ecotone between macrophyte-formed habitat and bare substrate, current flow and turbulences are reduced. This may cause accumulation of swarming hyper-benthic invertebrates (such as mysids) and therefore offer a great opportunity for juveniles to forage (Macreadie et al., 2010).

Edge effect may also come from the complementarities of resources level proper to each habitat. At ecotone, organisms (mobile especially) may regularly switch between habitats and therefore exploit alternatively the optimum habitat as regards to the resource expected

(basically food or shelter). For instance, one habitat may be optimum for foraging activities but with a higher predation risk than another habitat. At the ecotone, juveniles can therefore forage efficiently in the risky habitat and switch when a predator is detected (see Box 6). Interaction between predator tactic and structural complexity may also result in positive edge effect for prey juveniles which have developed adaptative anti-predator behavior (Matsuda et al., 1993). Positioned close to the ecotone between a highly complex habitat and an open habitat, juveniles may escape into the suitable habitat as regards to the tactic of the predator detected (see section above for details about habitat-specific predators) (Martin et al., 2010; Smith et al., 2011).

Box 6: An example of an experiment testing juveniles response to interactive effects of habitat and seascape configuration: abundance patterns suggest edges effect - from Cheminée et al. (in prep)[3].

Cheminée et al. (*in prep*) compared densities of *Coris julis* juveniles between two habitats (*Cystoseira* Forest and Dictyotales Bush) and two seascape configuration (wide habitat, i.e. covering at least 16m² and patchy habitat, i.e. 4m² area interspersed with the other habitat). Densities were higher in wide Dictyotales habitats than in wide *Cystoseira* habitats. This suggests a better survival and/or active selection due to differential habitat quality. Moreover, densities were higher in patch of Dictyotales close from neighboring canopy forming *Cystoseira*, than in wide Dictyotales far from any canopy forming habitat. This suggests edge effect. Based on knowledge about *C. julis* feeding habits (Guidetti, 2004; Stergiou and Karpouzi, 2001), Dictyotales Bush offers better food resources and the putative edge effect might therefore come from the better value of *Cystoseira* forest as shelter against predators.



[3] See Chapter IV part 2

From habitat- to seascape-based management

We highlighted that analysis and understanding of juvenile settlement patterns have to consider nested sets of seascape features. At a wide spatial scale, oceanographic patterns affect larval dispersal and consecutive broad patterns of juvenile settlement. At a finer spatial scale, structural complexities of habitats affect their quality (basically food availability and predation risk), which drives local patterns of juvenile settlement through differential mortality and active habitat selection.

These theories and experiments about causal mechanisms were put forth by worldwide studies but Mediterranean examples are too scarce; existing studies only highlight distribution patterns. This stresses the need to trigger similar research programs in Mediterranean countries in order to better understand all the underlying mechanisms acting at nested spatial scales and ultimately draw a comprehensive scheme at the seascape scale.

Globally, worldwide researches presently synthesized all support that complementarities and synergies occur between habitats of a seascape; the whole mosaic must consequently be taken into account for management practices. After decades of local-scale habitat-focused management, it is now required to upgrade coastal management to a wider seascape approach.

References

See Chapter references

3.5.3 Differential habitat use, anti-predator behavior and mortality of juvenile Symphodus spp. (Pisces : Labridae) in response to multiple functional types of fish predators

Thiriet, Cheminée, Branthomme, Escoubet & Francour, in prep.

In the previous part, Box 4 presented an example of an experiment evidencing the interaction between predation success and habitat architectural complexity. This study was performed in 2011 in the frame of a Master student thesis, Samuel Branthomme. Along with Pierre Thiriet and Patrice Francour, I co-supervised this student during his field work, *ex-situ* experiments, and writing. Data are currently being more deeply analyzed in order to submit a paper for publication. Here under is a copy of the abstract of this Master thesis, defended in September 2011 at Aix-Marseille University.

Abstract of Samuel Branthomme Master thesis

"Some habitats of the Mediterranean Infralittoral act as a nursery for juvenile fishes, but they may be altered by many human-induced alterations. Thus, it is essential to identify potential nursery habitats and the consequences of their alterations on this function. Two alternative hypotheses tend to explain the differences in juveniles abundance between habitats with varying complexity: (1) predators are more effective in less dense habitat and (2) juveniles make an active choice to take refuge in more complex habitats. To investigate these hypotheses, we analyzed the survival time and behavior of juvenile *Symphodus ocellatus* within ex-situ habitats of varying complexity (*Cystoseira* forest, Dictyotales grassland, mixed forest/grassland habitat, bare substratum), in the presence of two types of predators: a stalk-and-attack predator (*Serranus cabrilla*) and a sit-and-wait predator (*Scorpaena porcus*). First, it appears that the survival time of juveniles increases with habitat complexity. Secondly, juveniles display a thoughful choice to seek refuge in complex habitat, this choice being affected by the type of predator: *S. cabrilla* pushes juveniles to seek refuge more distinctly in the forest, but they go out of the forest when *S. porcus* is around. In the same way, micro-habitats occupied by the juveniles in homogenous habitats (i.e. not mixed) changes with the type of predator: juveniles hide within the forest or the grassland when *S. cabrilla* is around, whereas they rise into the water column when *S. porcus* is around. Thus, our results suggest that ex-situ differential mortality and active choice of habitat are both responsible of differences in juveniles densities observed *in-situ* in their natural habitats."

3.5.4 Supplementary data : empirical observations illustrating edge effect

Part 3.5.2 explain how processes driving abundances patterns, when acting at the ecotone between adjacent habitats, may lead to some edge effects. Here I present some pictures of empirical observations of this edge effect, taken during my PhD's field work in the Bay of Villefranche (French Riviera).

In my study area, from 2009 to 2011, I regularly explored various habitats surrounding the artificial habitat experiments I was monitoring (Chapter III-part 2 and Chapter IV-part 2). While doing so I consequently gathered empirical observations, namely of some fish juvenile or young individuals behavior that may illustrate edge effects. The mosaic of juxtaposed habitats I regularly visited was situated in a depth range of 0 to 4 meters and was composed of: shallow blocks and pebbles, wide seagrass meadows (*Posidonia oceanica*), medium-sized (100 m²) denudated sandy areas or dead matte of *Posidonia* (Fig. 1), and large blocks.

In April-June of each year, juveniles (about 20 mm TL) of *Spondyliosoma cantharus* (Fig. 1a) and *Diplodus annularis* (b) were regularly observed at the edge between sand and seagrass. During June-July, *Pagrus pagrus* juveniles (about 20-35 mm TL) were mostly observed at this edge, or at the limit between seagrass and dead matte (c) as were early settlers of *Coris julis* (10-15 mm TL) in August; these last ones, when present on the canopy-forming artificial habitats (Chapters III-2 and IV-2) were mostly spotted at the artificial canopy-habitat edges (d). The juveniles of the predator *Serranus hepatus,* when observed (from 15 to 55 mm TL, during June-August), were systematically seen at the edge of artificial canopies in a 2010 pilot patch-size experiment (e), and so were the few observed *Dentex dentex* juveniles (20-25 mm TL) (f). The smallest observed *Serranus cabrilla* juveniles (g) (30-40 mm TL, in June) were mostly observed at the edge of canopy forming habitats (g: here *Posidonia oceanica*), while young individuals (about 70 mm TL) were observed actively searching for preys at the edges of natural *Cystoseira* forests in Corsica (h).

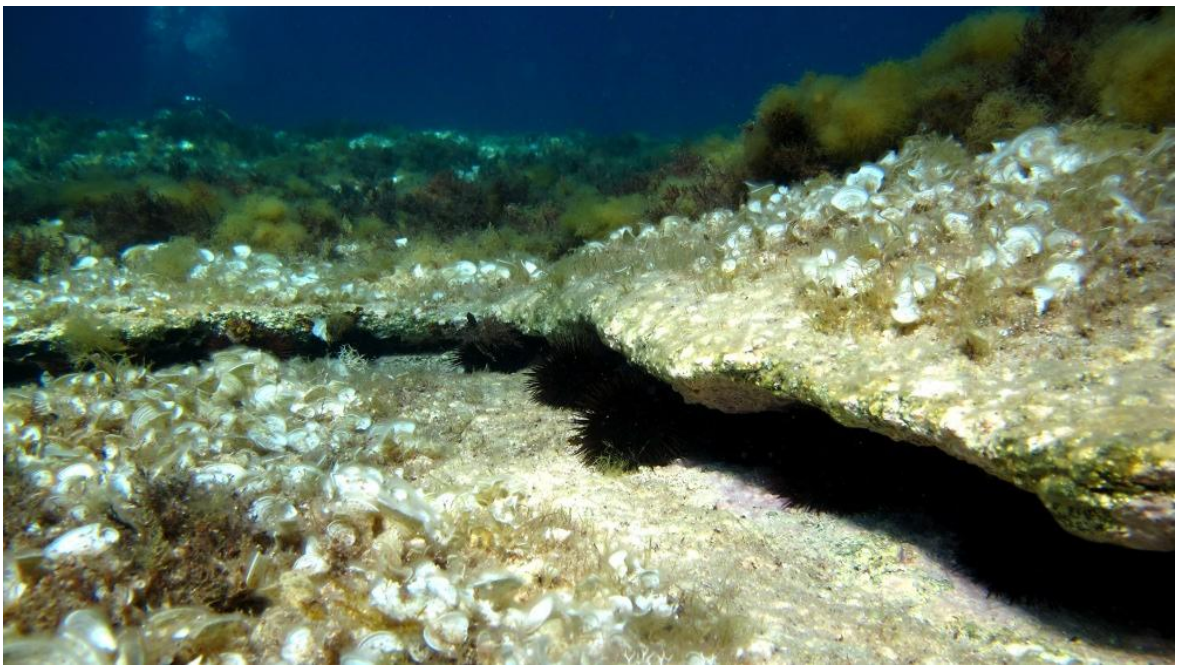
Fig. 1. Empirical observations of edge-effect induced-behavior, see detailed explanations in the text (left page)

3.6 Chapter conclusions

- We assessed and highlighted the high nursery value of *Cystoseira* forests for some species of coastal fishes, including species of commercial interest, in comparison notably with the Dictyotales – Sphacelariales (DS) bushy assemblage habitat.
- Taxa specific abundance pattern (notably for *Symphodus* spp., *Coris julis*, *Serranus* spp. and *Labrus* spp.) across habitats (*Cystoseira* forest *vs.* DS bushland) were consistent through time (over at least two years) and through space in the Ligurian Sea: over 20 km in 20 sites displaying natural habitats of Corsica and over 180 km if considering as well artificial habitat experiments along the French Riviera.
- As observed previously for *Diplodus* spp. (Chapter II) we highlighted notably for *Symphodus* spp. a strong spatial variability of its juvenile densities in *Cystoseira* forests at both local (sites, 1 km) and regional (locality, 20 km) spatial scales. This spatial variability was partially correlated to environmental (biotic and abiotic) factors (such as depth, canopy height).
- According to our *ex-situ* experiments, both differential mortality and active habitat selection drive the *Cystoseira* forest juvenile fish densities. Lower predation success in the forest, probably due to its structural complexity, appeared to be one of the factors explaining the reduced mortality in the forest for *Symphodus* spp. juveniles. Refuge availability, as a function of tri-dimensional structure of the habitat, seemed consequently to be a main driver of *Cystoseira* forests nursery value for these species. However influence of food availability remains to be explored (see Chapter VI, perspectives). Given our *in-situ* observations, *Serranus* and *Coris* juveniles seemed to rely on *Cystoseira* habitats more particularly through edge effects e.g. for hunting preys (*Serranus*) or sheltering (*Coris*) in the forest. This will be highlighted in Chapter IV.
- Preliminary results suggested more research is needed to compare the relative nursery value of *Cystoseira* forest *vs. P. oceanica* meadows and other habitats of the seascape mosaic (see perspectives in Chapter VI).

As a conclusion, based on these first results about nursery value across various habitats of the infralittoral, further studies of (1) nursery value of other unstudied habitats of the seascape mosaic, (2) processes explaining site specific variations of a given habitat nursery value, associated to (3) detailed cartography of the various state of the biocenosis of photophilic macrophytes of the rocky Infralittoral (up to now designated by “Natura 2000” legal framework under a unique category), will allow to better target conservation efforts of essential fish nursery habitats (Beck et al., 2001). Finally, depletion of these *Cystoseira* forests (e.g. reduction of canopy density or patch-size) may strongly affect the recruitment of several species of littoral fishes. In order to test this hypothesis, the use of artificial *Cystoseira* thalli appeared as an accurate method to manipulate *in-situ* habitats. Threshold levels of forest depletion (Worthington et al., 1991) could not be find in the preliminary 2009 experiment: the next Chapter (IV) explores these questions more deeply.

Chapter IV. Consequences of habitat transformations on their nursery value



Punta Spano (-4 meters), Calvi Bay, Corsica, 15 of July 2010 – Near from the refuge offered by crevices, sea-urchins maintain a grazed area cleared of the *Cystoseira balearica* canopy

Chapter IV. Consequences of habitat transformations on their nursery value

4.1 Chapter introduction

In chapter I we highlighted that *Diplodus* spp. nursery habitats (the shallow and sheltered bottoms of blocks and pebbles) are rare along rocky shores of the Mediterranean. In Chapter II we highlighted that *Cystoseira* forests have a high nursery value for Labridae juveniles e.g. *Symphodus* spp. Both these Mediterranean rocky Infralittoral habitats are located in the upper Infralittoral, which make them particularly vulnerable to human induced transformations (Coll et al., 2010) and modification of their tri-dimensional structure, *sensu* August (1983)[4]. Given their functional importance for the replenishment of littoral fishes (Beck et al., 2001) and their vulnerability, a better understanding of the potential effects of habitat transformations on their nursery value is necessary.

In the present chapter we aimed at studying the effect on juvenile fishes of two types of habitats transformations that are currently occurring in the Mediterranean: the alteration of *Cystoseira* forests and the homogenization of rocky bottoms by the spread of the invasive macrophyte *Caulerpa taxifolia*.

This chapter is organized in two articles in preparation for submission:

- Part 4-2: “Consequences of density decrease, patch size reduction and fragmentation of *Cystoseira* forests on their nursery value for Mediterranean juvenile fishes”
- Part 4-3: “Does loss of habitat heterogeneity and complexity alter fish recruitment? Preliminary results from the Mediterranean example of *Caulerpa taxifolia* invasion”

4.2 Consequences of density decrease, patch size reduction and fragmentation of Cystoseira forests on their nursery value for Mediterranean juvenile fishes

In prep.

Note:

In the following paper (in prep.) pictures have been inserted as supplementary illustration of M&M although they will not be displayed in the version submitted for publication.

[4] See Chapter VI for a discussion on habitat tri-dimensional structure (heterogeneity and complexity) *sensu* August (1983)

Consequences of patch-density decrease, patch-size reduction, and fragmentation of *Cystoseira* forests on their nursery value for Mediterranean juvenile fishes

In prep.

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Analyzed the data: AC, PT
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INTRODUCTION

In the Mediterranean, a dramatic decline of the formerly widespread *Cystoseira* forests has been observed along rocky shores (Thibaut et al., 2005). In the North-Western Mediterranean, this decline is notably due to a combination of anthropogenic pressures, and has been particularly described along the Spanish, French and Italian continental rocky shores (Mangialajo et al., 2008; Sala et al., 1998; Sales et al., 2011; Thibaut et al., 2005). These canopy-forming species used to create wide and continuous forests, covering at 80 up to 100 % percent cover large areas of the rocky Infralittoral (Ballesteros, 1992; Clarisse, 1984; Hoffmann, 1988; Hoffmann et al., 1992). Nowadays, such wide and continuous cover of *Cystoseira* forests can only be found in some areas, notably along the rocky shores of e.g. Corsica or Menorca Islands (Ballesteros et al., 2010; Ballesteros et al., 2002; Ballesteros et al., 1998; Sales and Ballesteros, 2009; Sales and Ballesteros, 2010; 2012; Sales et al., 2012). In the near future these remaining forests may as well be subject to habitat transformations, e.g. in case of massive spread of herbivorous such as sea urchins or the invasive herbivorous fish *Siganus* spp. which already caused severe overgrazing of rocky bottoms in the eastern Mediterranean (Sala et al., 2011). *Cystoseira* forests transformations implies notably (1) a decrease of the canopy density and of patch-size; and consequently (2) a fragmentation of the wide forests into a mosaic of patchy habitats (Ballesteros et al., 2010; Ballesteros et al., 2002). A previous study[5] (Cheminée et al., under review) highlighted and quantified for the first time the high nursery value -*sensu* Beck *et al.* (2001)- of *Cystoseira* forests for some species of littoral fishes of ecological and economical importance. The habitat "nursery value" is defined as "the production of individuals that recruit to adult populations per unit area of juvenile habitat" and therefore a habitat plays a "nursery role" for juveniles of a given specie if its nursery value is greater on average than in other habitats in which juveniles occur (Beck et al*.,* 2001). A proxy of the nursery value of each habitats can be assessed by measuring its first of four components (Beck et al., 2001) i.e. densities of juveniles per habitat area. Refuge availability seemed to be the main driver of forests nursery value (Cheminée et al., under review). Consequently decrease of the canopy density and of patch-size and the consequent fragmentation of wide forests into a mosaic of patchy habitats may strongly affect the recruitment of these fishes. The previous study was not able to determine the threshold canopy cover density level at which fish juvenile densities may be affected (Worthington et al., 1991) since no significant differences of juvenile *Symphodus* spp. densities appeared between the 100% and the 60% cover density treatments. The present study investigates the effects of these habitat transformations on the nursery value of *Cystoseira* forests, by studying fish juveniles in (1) artificial habitats designed such as to reproduce various levels of alteration of *Cystoseira* forest patches and (2) natural habitats of

[5] See Chapter II-part 2

Corsica (Fig. 1) were both wide and fragmented forest could be found. These habitats were tested for their effects on fish juvenile assemblage's composition, species richness, total and taxa-specific abundances, sizes and behavior. The ultimate objective was to estimate the threshold forest parameters (canopy cover density, patch size and degree of fragmentation) at which fish settlement and recruitment collapses (Bell et al., 1987; Worthington et al., 1991).

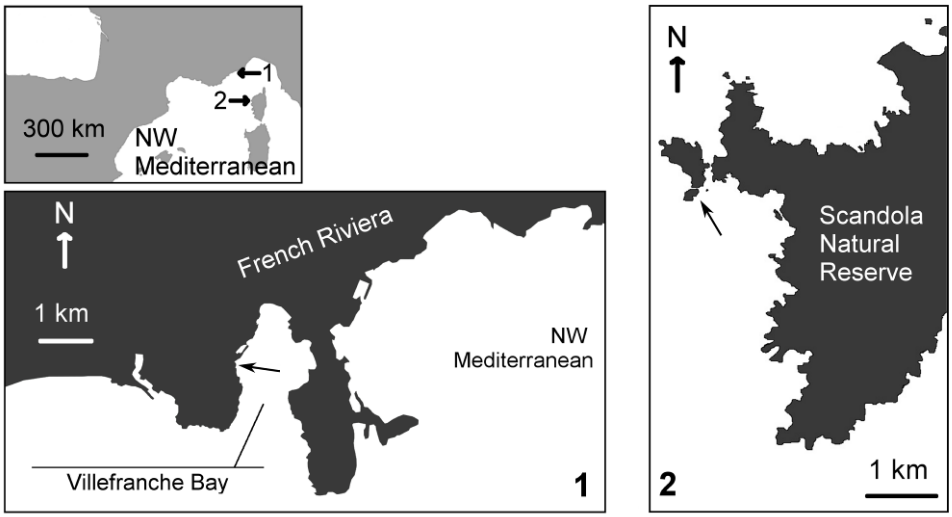
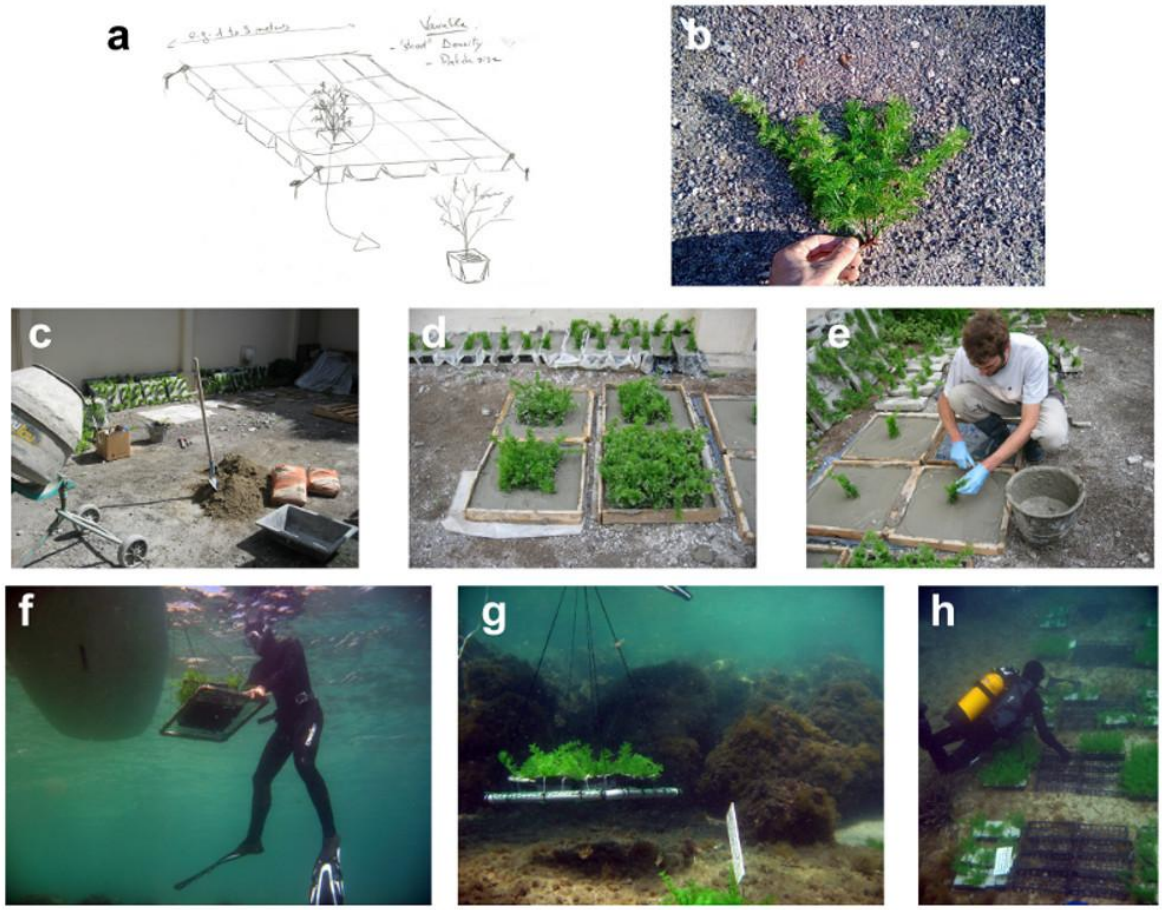


Fig. 1. Study locations (signaled by arrows). [1]Villefranche Bay, southern France: 43° 41' 42,77'' N, 7° 18' 28,10'' E (patch-density and patch-size manipulative experiment); [2]Garganellu Islet, Scandola Natural Reserve, Corsica: 42° 21' 55,00'' N, 8° 32' 25,00'' E (wide *vs* fragmented natural *Cystoseira* forests)

MATERIAL AND METHODS

Patch-density and patch-size effects tested in artificial habitats

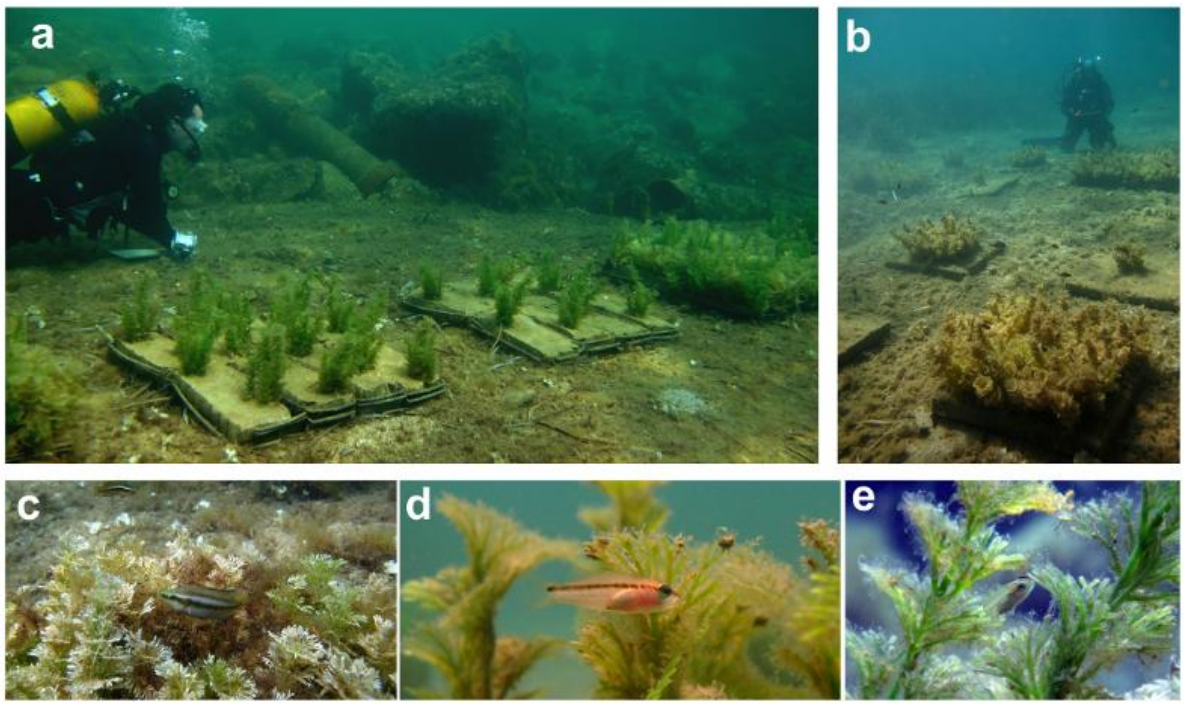
To test the effect of the alteration of the *Cystoseira* forests on Mediterranean juvenile fish assemblages, we created artificial habitats mimicking various degrees of alteration of a *Cystoseira* forest in Villefranche Bay, France (Fig. 1). We conducted a manipulative experiment with artificial habitats studying the effects of *Cystoseira* forests patch-density and patch-size on its nursery value. The use of artificial habitats mimicking *Cystoseira* forest was proven efficient in a previous study (Cheminée et al., under review), in which, as in other studies about Fucales (e.g. Sargassum) (Godoy and Coutinho, 2002; Ornellas and Coutinho, 1998; Shulman, 1985), these artificial macrophytes attracted assemblages of fishes similar to those found in natural habitats. Two separate experiments where set up in order to test for the two chosen parameters reflecting the most *Cystoseira* forest depletion: patch-density and patch-size. Artificial habitats were built similarly as in Cheminée et al. (under review), where artificial plastic *Cystoseira* thalli (ACY) are fixed on a flat concrete base as to reproduce a canopy forming *Cystoseira* patch over a rocky substratum (Photo-panel A and B). Artificial sampling units (ASU) were made of either (1) various cover density or (2) various patch-size, i.e. treatments mimicking forest from the healthiest to the most depleted. For the patch-density experiment, patch-size was constant among treatments (i.e. square-shaped patch of 0.5 m^2) and factor "density-treatment" had four density levels: dense (D1-D, i.e. 100%, continuous cover with 160 ACY m^{-2}), sparse (D2-S, 32 ACY m^{-2} i.e. about 30% cover) and very sparse (D3-VS, 16 ACY m^{-2} i.e. about 15% cover). A fourth treatment corresponded to bare substratum (D4-B), with no ACY and only short turf composed of Dictyotales and Sphacelariales with 72% mean cover (Max: 80, Min: 60, n = 3) and 2.9 ± 0.3 (SE) cm mean height (n = 30). For the patch-size experiment, cover density of patches was constant among treatments (i.e. continuous cover with 160 ACY m^{-2}) and factor "size-treatment" had six levels: Very large patch (S1-VL, i.e., 0.50 m^2), large (S2-VL, i.e., 0.23 m^2), medium (S3-VL, i.e., 0.10 m^2), small (S4-S, i.e., 0.03 m^2), very small (S5-VS, i.e., 0.01 m^2). A sixtieth treatment corresponded to bare substratum only (S6-B), with no ACY and only short turf composed of Dictyotales and Sphacelariales. For both patch-density and patch-size experiments, ACY thalli had a mean height of 17 cm (min = 12, max = 22, n = 30); each treatment had three replicates. All replicates were placed at 2.5 meter depth in the same experimental area, located in the same site than in the previous study (Cheminée et al., under review) in the Villefranche Bay (Fig. 1.1). See Material & Methods therein for more details on ASU building and experimental design.



Panel. A. Building of artificial sampling units and setting up of the experimental design – a: initial prototype drawings, b: Artificial *Cystoseira*; c to e: steps of preparation ; e : building treatment "Very-small" ; f to h : underwater settlement of the density experiment in 2009 (first prototype).

ASUs were deployed at the beginning of spring 2010 (for patch-density experiment) and spring 2011 (for patch-size experiment), in early April, after main winter storms and before the beginning of the settlement period for most studied species, which takes place mainly between May and September as observed during our previous experiment (Cheminée et al., under review) and in other studies (Froese and Pauly, 2011; Garcia-Rubies and Macpherson, 1995; Lejeune, 1985; Raventos and Macpherson, 2001). This allowed artificial *Cystoseira* to gather epibiota and resemble the most possible to natural thalli (Panel Bb and Bc). Each year, from the end of April to the end of October, we conducted weekly underwater visual censuses (upon meteorological conditions) to monitor juvenile fish assemblages at each ASU (Photo Panel B): during daylight (between 10am and 4pm), two previously inter-calibrated divers (AC and JP in 2010, AC and PT in 2011) recorded the abundance and size (total length (TL); ±0.5 cm) of juvenile fishes present within each ASU, during five minutes. TL is hereafter identified by its lower size-class limit (e.g. 10 mm = 10 – 15 mm size class) (Cheminée et al., 2011; Cheminée et al., under review; Francour, 1999; Harmelin-Vivien et al., 1985; Harmelin-Vivien et al., 1995). Moreover, behavior of each individual during these five-minutes was

recorded: “behavior” factor had three levels, “permanent” (i.e. either “cryptic” or “deambulatory”) and “temporary”. Cryptic individuals where strictly associated with the ASU and hiding between thalli (see photo panel Be), never standing into the open water column; deambulatory individuals although not cryptic were tightly associated to the ASU, wandering long periods of time on it (at least or more than 30 consecutive seconds) (see photo panel Bd); temporary individuals would spend only short periods of time on the ASU (strictly less than 30 consecutive seconds). Rough sea and poor visibility days were avoided.



Panel. B. The ASU once deployed – a: patch-density experiment (2010); b: patch-size experiment (2011); c: adult *Symphodus ocellatus* taking care of its nest on a Very-large treatment (2011-06-08); d: a “deambulatory” juvenile of *Serranus cabrilla* (30 mm TL, 2010-06-24); e: a “cryptic” juvenile of *S. ocellatus* (25 mm TL, 2010-07-01) hiding between ACYs.

According to previous studies (Cheminée et al., under review; Garcia-Rubies and Macpherson, 1995) fish juvenile families we expected in these habitats belonged more particularly to the Labridae and Serranidae families. Nevertheless, our sampling took into account all necto-benthic and crypto-benthic juvenile species encountered. The smallest specimens of the species observed were considered newly settled individuals. For most rocky reef fishes in the Mediterranean, size at settlement is around 10 mm TL (Garcia-Rubies and Macpherson, 1995). For each taxa, all individuals smaller than one third of adult maximum total length (Louisy, 2002) were considered as young of the year (y_0) or young of the past year (y_{+1}) (Table 1 in results).

Forest fragmentation effects tested in natural habitats

The effect of *Cystoseira* forest fragmentation on its nursery value was studied during the first week of August 2010, by comparing the juvenile fish assemblages of four habitats present next to Garganellu islet, within the Scandola Natural Reserve, in Corsica (Fig. 1.2) : wide forest of the canopy forming *Cystoseira brachycarpa* J. Agardh var. *balearica* (Sauvageau) Giaccone (hereafter *C. balearica* for simplicity), patches of *C. balearica* forest, patches of shrubby assemblage (Dictyotales and Sphacelariales = DS), wide area (bushland) of shrubby assemblage (DS). Wide habitats covered continuously more than 16 m² and patchy habitats sized about 4 m². A detailed description of these habitats characteristics can be found in Ballesteros et al. previous works (Ballesteros et al., 2010; Ballesteros et al., 2002). The depth range of the study was between 3 and 8 meters, where settlement is commonly observed for Mediterranean coastal fish species and where *C. balearica* have their optimum growth (Ballesteros et al., 2010; Ballesteros et al., 2002; Sales and Ballesteros, 2009; Sales and Ballesteros, 2010). A SCUBA diver (AC, OB, JMC) slowly swam and haphazardly selected 8 sampling points within each of the 4 studied habitats. Substratum type (flat rock with few crevices) and slope (gentle, i.e. < 30°) were kept constant. At each sampling point the observer recorded macroalgal species percent coverage and mean canopy height (n = 8) in 1 m² plot (Cheminée *et al.*, under review). The diver recorded the abundance and size of juvenile fishes within each 1m² plot during five minutes on a submersible plastic slate as described for artificial habitats.

DATA TREATMENT

Effects of treatments on juvenile assemblage: composition, richness, total density of juveniles

Multivariate exploratory approach

Effects on juvenile assemblage composition were first studied through a multivariate exploratory approach using both a hierarchical complete-linkage agglomerative clustering method (CLUSTER) and non-metric multi-dimensional scaling (nMDS) (Clarke and Gorley, 2006). Resemblance measure matrixes were calculated from the initial data matrix containing for each sample (census done on each treatment replicates) the abundance of juvenile for each species. The chosen resemblance measure was the binomial deviance (scaled) dissimilarity measure (Anderson and Millar, 2004); CLUSTER routine was used to explore potential grouping structures among the samples: its output is a dendogram, i.e. a tree diagram displaying the grouping of samples according to given levels of dissimilarity. Complete-linkage was preferred given its synoptic properties, i.e. adapted to a global assemblage description in treatments (as opposed to single-linkage). nMDS represents samples as points in low-dimensional space such as the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples. Grouping factors where used to generate centroids for given combination of factors, i.e. an “average” point e.g. for all replicate of a given treatment within a month. A new resemblance matrix was then generated using the grouping factor (e.g. “month-treatment”) and calculating the new dissimilarities between centroids of factor “month-treatment”. This allowed displaying clearer graphs showing only summarized data. Clusters generated by slicing the dendograms at levels showing the biggest change in dissimilarity were overlayed on nMDS plots to facilitate graphical interpretation. For nMDS plots, as visual aids, months were afterwards grouped by “season” as follow: “spring” (April, May, June), “summer” (July, August), “fall” (September, October). I choose this grouping because we know that there is a temporal partition of taxa settlement, since biological cycle (reproduction) are induced notably by temperature and light conditions, which vary along seasons. Finally, for each taxa (specific abundances) correlation of taxa-specific density with the 2-D ordination plot of samples were plotted by displaying correlation vectors. Spearman correlation was used given its non parametric properties.

Multivariate inferential approach

Our hypothesis was that the global composition of juvenile fish assemblage would differ between levels of factor “treatments” (both patch density and patch-size experiment) and between levels of factor “habitat” (fragmentation study in natural habitats). Distribution of densities within our data contained many zeros and was highly skewed. Even after log-transformation it did not fit the normality assumption. In order to compare juvenile densities as a function of the various factors of our design, we thus decided to perform PERmutational

Multivariate ANalysis Of VAriance (PERMANOVA) (Anderson, 2001) based on the binomial deviance (scaled) dissimilarity measure, as for the NMDS, which make this non parametric test the equivalent of a parametric MANOVA but free from the assumptions of normality and homoscedasticity of residuals (Anderson, 2001). P-values were obtained by 9999 permutations of residuals under a reduced model. Monte Carlo P-values were considered when there were not enough possible permutations (<200). In order to compare assemblage densities between levels of factors we performed the PERMANOVA on the model including terms and all interactions (Underwood, 1981) and terms were then pooled as suggested by Anderson et al. (2008).

A model was fit to assemblage densities in order to test its response to treatment, month and census. Densities were modeled as a function of 3 factors: factor “month” has 7 or 6 levels (April to October 2010 and May to October 2011) and is fixed; Factor “census” has 22 (2010) or 20 (2011) levels, it is random and nested in Factor “month”; factor “treatment” has 4 levels in the patch-density experiment (2010) (Dense (D1-D), Sparse (D2-S), Very-sparse (D3-VS), Bare (D4-B)) and has 6 levels in the patch-size experiment (2011) (Very-large (S1-VL), Large (S2-L), Medium (S3-M), Small (S4-S), Very-small (S5-VS), Bare2 (S6-B)) and is fixed. Since ecological data are by nature highly variable, terms were considered significant for P-values < 0.1

Univariate inferential approach

For the same reasons as previously we preformed PERmutational univariate ANalysis Of VAriance (PERANOVA) on each of some variables related to the description of the assemblages : total abundance of juveniles (all species pooled) and species richness; species richness was subdivided in two response-variables: 1) annually cumulated richness per treatment (n replicates = 3) and 2) richness per treatment and per censuses (n censuses = 22 (2010) and 20 (2011) ; n replicates = 3).

In order to compare each of these variables (all taxa total density, richness) between levels of factors (treatment, census, month) we performed the PERANOVA on a model including terms and all interactions (Underwood, 1981) and terms were then pooled as suggested by Anderson et al. (2008).

A first model was fit to “total density” and “richness per treatment and per censuses” in order to test their response to treatment, month and census. Total juvenile density and richness were each modeled as a function of 3 factors: factor “month” has 7 or 6 levels (April to October 2010 and May to October 2011) and is fixed; Factor “census” and factor “treatment” had the same characteristics as previously.

A second model was fit to “annually cumulated richness per treatment” in order to test its response to treatment. Richness was modeled as a function of factor “treatment” which has the same characteristics than previously.

Taxa specific effects of treatments/habitats on juveniles

In order to compare each of our variables (taxa-specific density, TL) between levels of factors (taxa, size-class, treatment, census, month, behavior) we performed a PERmutational ANalysis Of VAriance (PERANOVA) on the model including terms and all interactions (Underwood, 1981) and terms were then pooled as suggested by Anderson et al. (2008).

For frequent taxa and other potential predator taxa, a first model was fit to total density per taxa in order to test the taxa-specific response of fish juveniles to treatment, month and census. Total juvenile density per taxa was modeled as a function of 4 factors: factor “taxa” has 6 levels (*Symphodus* spp. (i.e. *S. cinereus* excluded), *Symphodus cinereus*, *Coris julis*, *Serranus* spp., *Scorpaena porcus* and *Muraena helena*) and is fixed; Factor “month” has 7 or 6 levels (April to October 2010 and May to October 2011) and is fixed; Factor “census” has 22 (2010) or 20 (2011) levels, it is random and nested in Factor “month”; factor “treatment” has 4 levels in the patch-density experiment (2010) (as previously) and has 6 levels in the patch-size experiment (2011) (as previously) and is fixed.

For frequent taxa only , a second model was fit separately considering density per size class. Juvenile abundances were pooled among size classes i.e. for *Symphodus* spp. and *S. cinereus* : “small” (S = [10-30 mm[TL), “medium” (M = [30-50[mm TL) and “large” (L = [50-70[mm TL) ; for *Coris julis* : “small-medium” (SM = [10-40[mm TL) and “large” (L = [40-70[mm TL); for *Serranus* spp. : “small” (S = [30-50[mm TL), “medium” (M = [50-75[mm TL) and “large” (L = [75-100[mm TL). Putative effects of body size in fish relative to treatment, month and census were thus explored. This was not done for others taxa due to their lower abundances. In the second model, juvenile density per size class separately for each taxa was modeled as a function of 4 factors: factor “size classes” has 2 or 3 levels (small, medium, or small-medium, and large) and is fixed; Factors “month”, “census” and “treatment” have the same characteristics than previously.

For frequent taxa only, a third model was fit separately considering total length (TL) per species. Since the full design (with census and month) could not be balanced, juvenile TL was modeled as a function of only 2 factors: “taxa” and “treatment” which have the same characteristics than previously.

A fourth model was fit separately for *Symphodus* spp. only, considering density per behavior according to size class. Separately for each size classes (small, medium, large), juvenile density was modeled as a function of 3 factors: factor “behavior” has 2 levels in 2010 (permanent, temporary) and 3 levels in 2011 (cryptic, permanent, temporary; see definitions in M&M); Factors “month” and “treatment” have the same characteristics than previously.

For the natural habitat study, a fifth model was fit to total density per taxa in order to test the taxa-specific response of fish juveniles to habitats (4 levels: wide *Cystoseira* forests, patchy forest, wide DS bushland, patchy DS). A sixth model was fit separately considering density per size-classes. Juvenile abundances were pooled among size-classes as previously, and for Blenniidae-Gobiidae-Tripterygiidae according to: “small” (S = [10-25[mm TL), “smedium” (M = [25-40[mm TL) and “large” (L = [40-50[mm TL).

RESULTS

Settlement in the artificial habitat experimental area : observed species, settlement timing and size-classes patterns

Observed species

In the Bay of Villefranche, within the entire experimental area, during the two-year study period, 21 taxa were observed (Table 1). For further analysis some species were pooled as follows: *Symphodus* spp. (i.e. including *S. roissali* (Risso, 1810), *S. tinca* (Linnaeus, 1758) and *S. ocellatus* (Forsskal, 1775)) ; *Serranus* spp. (i.e. *S. cabrilla* and *S. scriba* (Linnaeus, 1758)) ; Blenniidae-Gobiidae-Tripterygiidae (crypto-benthic species). Some taxa amounted for a given year for more than 5% of the total amount of juveniles recorded in the experimental area (Fig. 2): they were considered as “frequent”, *versus* “occasional” taxa for the others (Table 1).

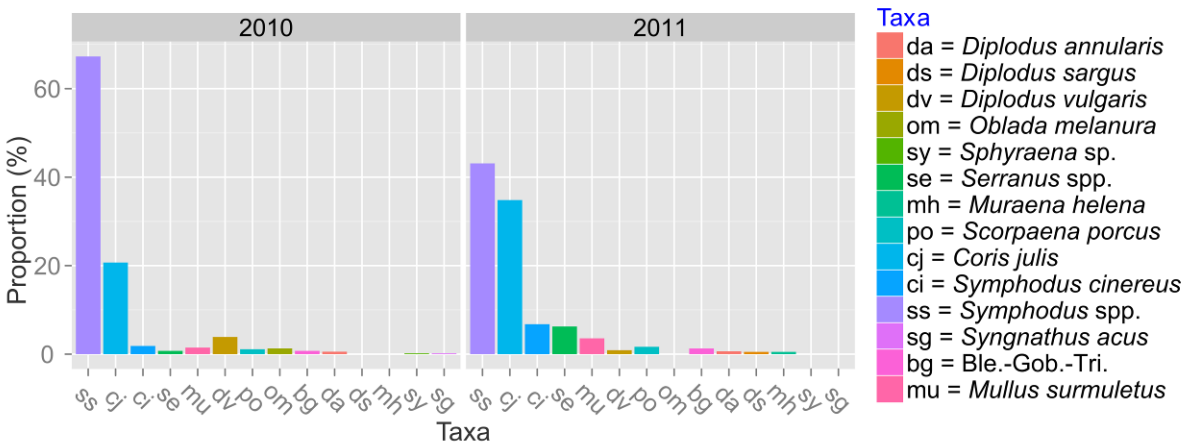


Fig 2. For each taxa, proportion of the total amount of juvenile individuals observed over each year

Table 1 : Observed juvenile taxa in the experimental area (2010 and 2011) - Definitions of y_0 and y_0 + y+1 size upper limits (see 2.1.2 in M&M) ; "-" = not defined in this study

		y0 upper limit (mm TL)	y0 + y+1 upper limit considered (mm TL)
Frequent taxa	*Symphodus* spp. (i.e. *S. ocellatus* (Forsskal, 1775), *S. roissali* (Risso, 1810) *S. tinca* (Linnaeus, 1758))	50	70
	Symphodus cinereus	50	70
	Coris julis (Linnaeus, 1758)	40	70
	Serranus spp. (i.e. *S. cabrilla* and *S. scriba* (Linnaeus, 1758))	75	100
Occasional taxa	*Diplodus vulgaris*	60	100
	Diplodus annularis	50	80
	Diplodus sargus	60	100
	Oblada melanura (Linnaeus, 1758)	-	100
	Blenniidae-Gobiidae-Tripterygiidae	-	50
	Mullus surmuletus (Linnaeus, 1758)	-	100
	Scorpaena porcus	-	100
	Muraena helena	-	500
	Syngnathus acus	-	140
	Sphyraena sp.	120	400

Settlement timing and size-ranges patterns

Settlement patterns through time appeared quite clearly and repeatedly both in 2010 and 2011 for the most frequent taxa: *Symphodus* spp., *S.cinereus*, *Coris julis*, *Serranus* spp. For these taxa, although timing may have slightly differed between years, size limits between y_0 and y_{+1} could be deduced from the following graphical representation of our data (Fig. 3, 5, 6 and 8) and were similar each year: as a consequence these data allowed us to refine the definition of y_0 size upper limit used for further analysis and presented in Table 1 (see explanations below).

For *Symphodus* spp., at the begin of both 2010 and 2011 study period (April to June) a cohort of y_{+1} individuals, of 50 mm TL and more, was present and was then joined in June by new settlers (y_0) of 10 mm TL (size at which we could detect them). This newly settled individuals then grew up until the end of the observation period (October), where they reached 45 to 50 mm TL, i.e. sizes near to those of y_{+1} individuals observed in spring (Fig. 3). When studying juveniles densities over the entire experimental area (all treatments pooled), both in 2010 and 2011, both census term (Fig. 4a,b, PERANOVAs, respectively $F = 8.55$, $p = 0.001$ and $F = 2.38$, $p = 0.004$) and interaction term between census and size class terms (Fig. 4, PERANOVAs, respectively $F = 3.04$, $p = 0.001$ and $F = 2.49$, $p = 0.001$) were significant: mean total *Symphodus* juvenile density per meter square increased from April-May to reach an abundance peak with its maximum densities in September (maximum mean observed of 14.0 ± 4.2 (se) ind. m^{-2} in 2010 and 6.3 ± 1.3 (se) ind. m^{-2} in 2011) and then started to decrease in October (Fig. 4a+b and pairwise tests therein). Both years, a first although less important peak of abundances occurred earlier in the summer, in June 2011 and (to a lesser

extent) July 2010 (Fig. 4a+b). When looking at densities per size-class, it appears that this first peak of abundances was composed mainly by “small” juvenile, i.e. early settlers ; besides in April and June observed individuals were mainly “large” ones, i.e. probably young of the past year (pairwise tests, Fig. 4c+d).

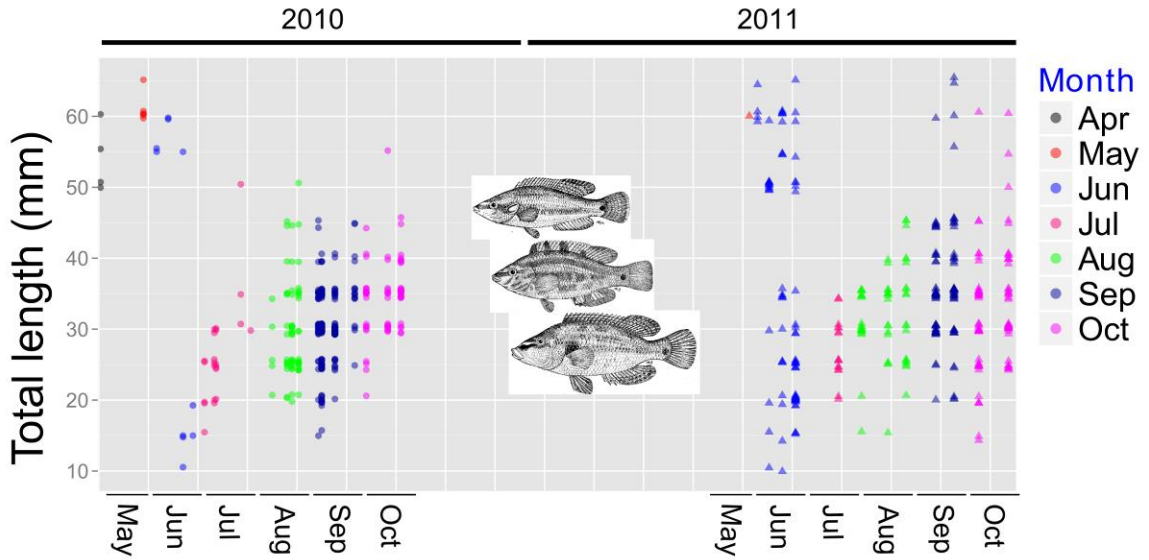


Fig. 3 : Symphodus spp. - total length (mm) of each individuals (1 dot = 1 individual) according to year and months

For *Symphodus cinereus*, in 2010 during the patch-density experiment, few individuals were observed in the experimental area (mean densities of 0 to 0.5 ind. m^{-2} per census). In 2011 during the patch-size experiment, census and month terms were slightly significant (PERANOVA, respectively F = 1.51, p = 0.096 ; and F = 3.22, p = 0.068): first individuals were observed end of june and reached a peak of abundance the third census of September with a mean of 2.2 ± 0.8 (SE) ind. m^{-2} over the full experimental area (Fig. 5a and 5b). Interaction term between month and size-class was significant in 2011 (PERANOVA, F = 3.82, p = 0.003): small individuals (<30 mm TL) were not observed over the experimental area. Almost only medium individuals were present from June to August in the experimental area (“post-settlers”, size when first observed around 30 mm TL) and then grew up as to reach the “large” size-classe, whose individuals were abundant only after the first census of September (Fig. 5c).

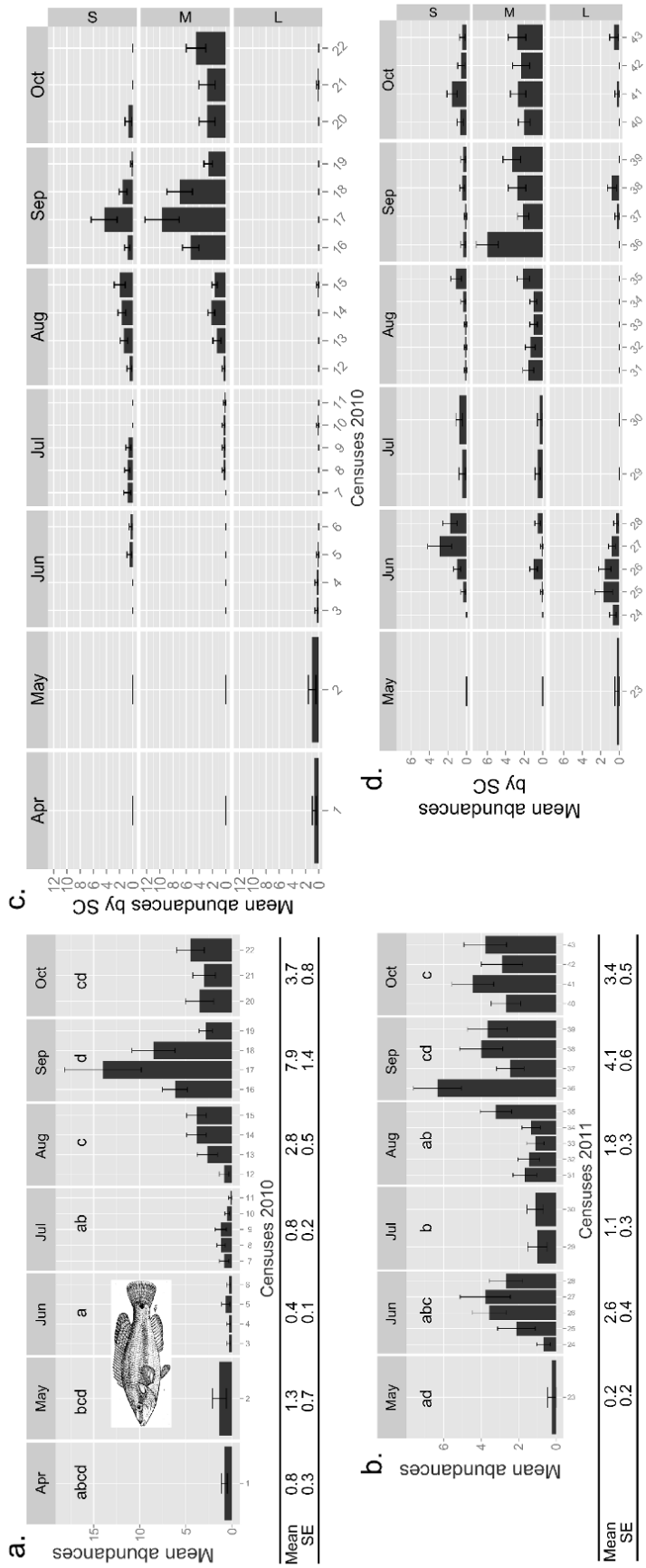


Fig. 4 ; a and b : mean (±se) of total *Symphodus* spp. densities (ind. m^{-2}) over the entire experimental area (all treatments pooled), for each censuses and by months; pairwise tests between months results are given (different lower case characters indicate significant differences between months) ; a: 2010, b: 2011 ; c and d: mean (±se) by size-classes: S (small), M (medium), L (large); see M&M for details.

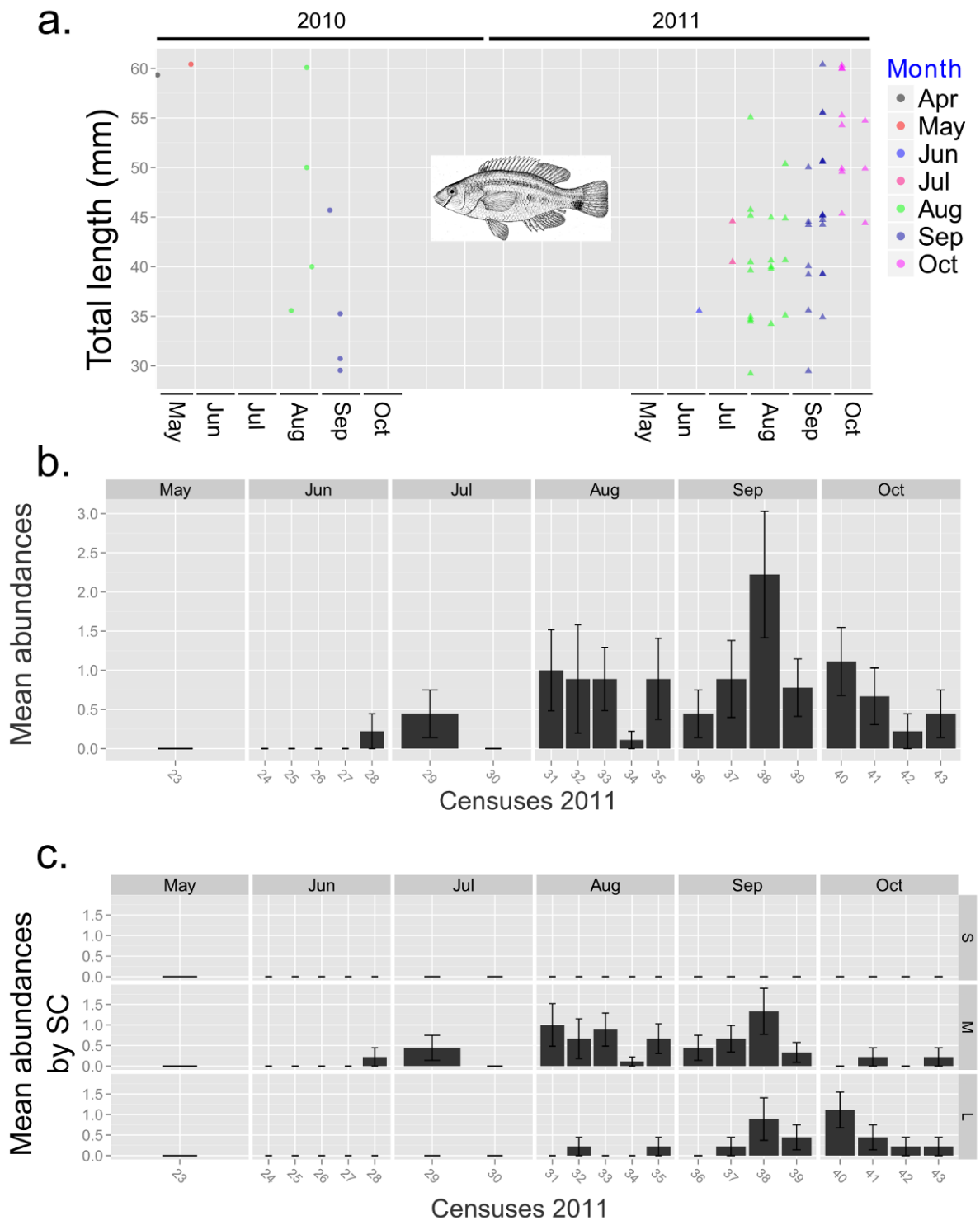


Fig. 5 ; *Symphodus cinereus* - a : total length (mm) of each individuals (1 dot = 1 individual) according to year and months b : mean (±se) of total *Symphodus cinereus* densities (ind. m-2) over the entire experimental area (all treatments pooled), for each censuses and by months; c: mean (±se) by size-classes: S (small), M (medium), L (large); see M&M for details.

For *Coris julis*, both years, a settlement pattern was observed similarly to *Symphodus* spp. but with slightly different sizes limits: in May-June y_{+1} individuals measured 40 mm TL and above, while y_0 individuals were first observed in June-July at 10 mm TL and grew up so that in October individuals ranged from 35 mm TL and above (Fig. 6). Both in 2010 and 2011, over the entire experimental area (all treatments pooled), mean *Coris julis* juvenile density per square meter increased from April-May to reach an abundance peak with its maximum densities in August (maximum mean density observed of respectively 1.7 ± 0.5 (se) and 6.1 ± 1.1 (se) ind. m^{-2}) and then started to decrease in September (Fig. 7a+b and pairwise tests therein). Both year interaction term between month and size class was significant (PERANOVAs, respectively $F = 5.84$, $p = 0.001$ and $F = 12.30$, $p = 0.001$): "small-medium" individuals (i.e. settlers) started to colonize the area in July and reached a peak abundances in August; few "large" individuals were present at the start of the monitoring period (i.e. young of the past year) and after august this class was gradually joined by growing recently settled juveniles ("small-medium") (Fig. 7c+d).

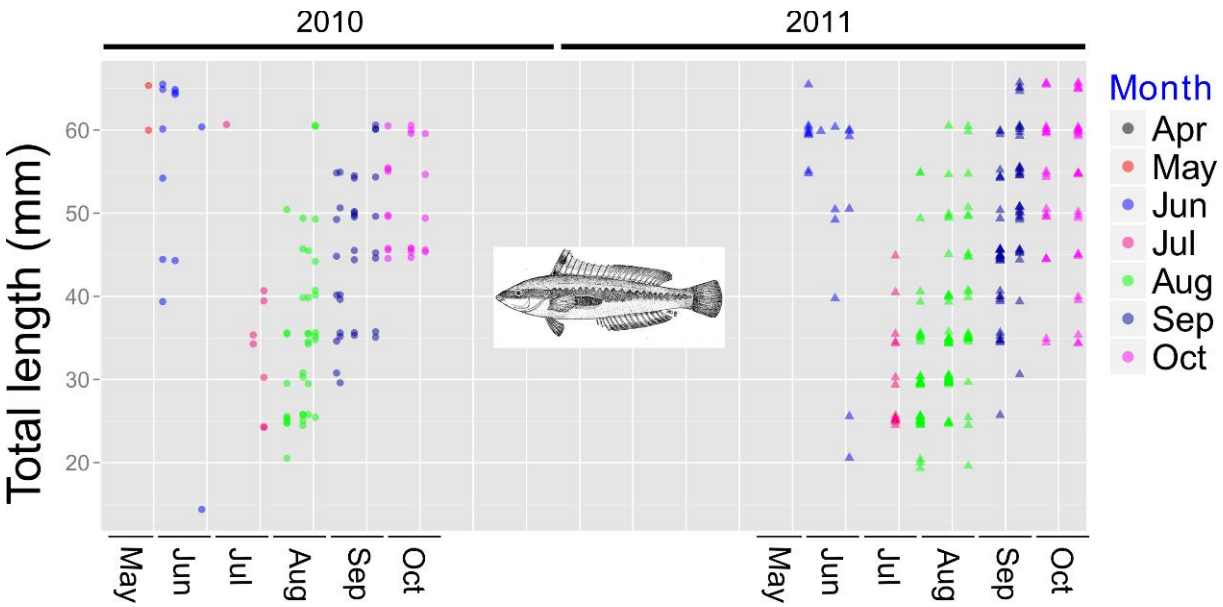


Fig. 6 : *Coris julis* - total length (mm) of each individuals (1 dot = 1 individual) according to year and months

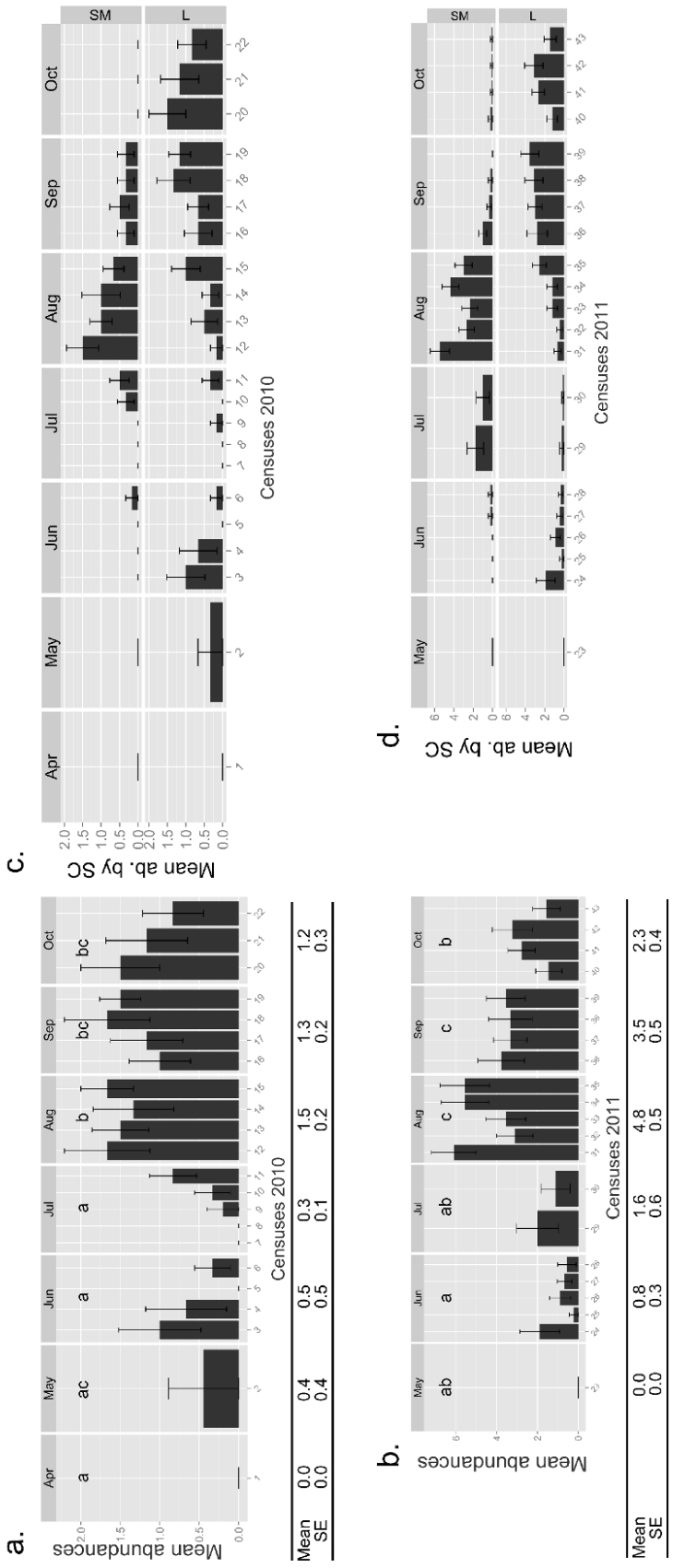


Fig. 7; a and b : mean (±se) of total *Coris julis* densities (ind. m^{-2}) over the entire experimental area (all treatments pooled), for each censuses and by months; pairwise tests between months results are given (different lower case characters indicate significant differences between months) ; a: 2010, b: 2011 ; c and d: mean (±se) by size-classes: SM (small-medium) and L (large); see M&M for details.

For *Serranus* sp., few individuals were observed in 2010. In 2011, interaction term between census and size-class was significant (PERANOVA, F = 2.03, p = 0.002) : only small individuals were present in June in the experimental area (size when first observed around 30 mm TL) and then grew up as to join the "medium" and "large" size-classes, reaching 80-90 mm TL in September-October (Fig. 8 and 9). y_0 and y_{+1} individuals could not be clearly distinguished in the study area.

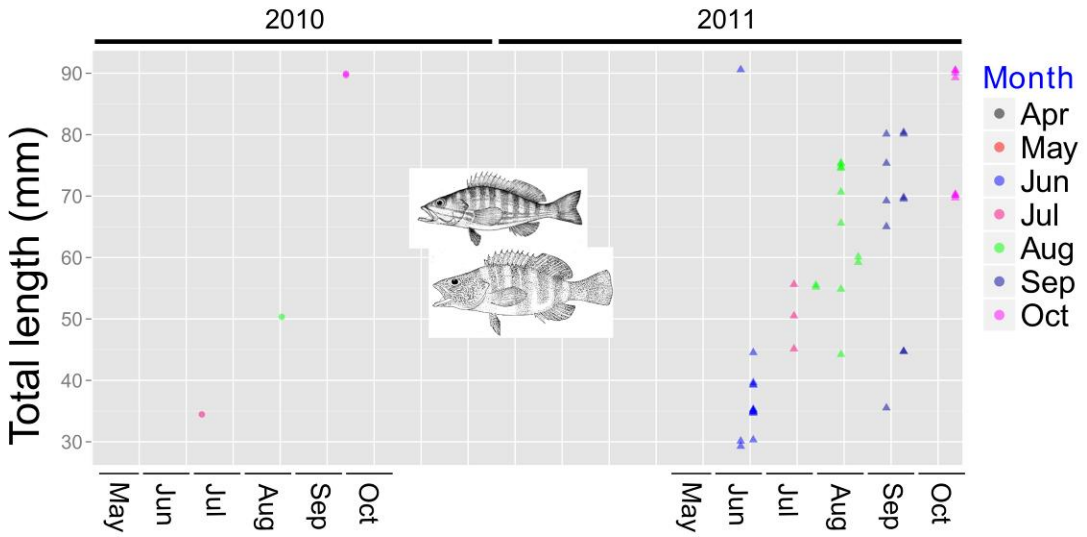


Fig. 8 - *Serranus* spp. - total length (mm) of each individuals (1 dot = 1 individual) according to year and months

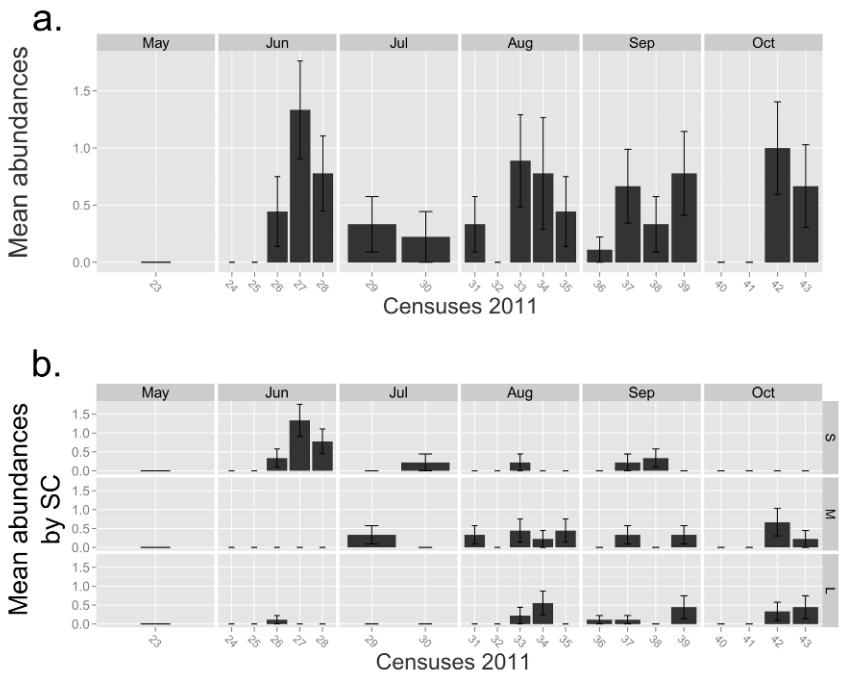


Fig. 9 ; a : mean (±se) of total *Serranus* spp. densities (ind. m^{-2}) over the entire experimental area (all treatments pooled), for each censuses and by months; b: mean (±se) by size-classes: S (small), M (medium), L (large); see M&M for details.

Patch-density and patch-size effects on juveniles tested in artificial habitats

Effects on juvenile assemblage: composition, richness, total density of juveniles

- Juvenile assemblage composition : multivariate exploratory approach

Dendograms (Fig. 10) were sliced at 0.7 and 0.85 respectively. Identified clusters (Fig. 10a) and the interpretation of MDS plots (Fig. 10b and 10c) showed two grouping trends, both for patch-density and patch-size experiments: samples grouped on one hand according to months and seasons and on the other hand trajectories along seasons differed according to treatments (Fig. 10c).

For patch-density treatments, one cluster gathered samples belonging to (a) spring AND a mix of all treatments while another cluster gathered samples belonging in majority to (b) spring and to the less depleted treatments (Dense and Sparse). Three other clusters gathered samples belonging in majority to fall (and summer) and respectively to (c) not-depleted forests, (d) intermediate levels of depletion forests and (e) bare substratum.

For patch-size treatments, two cluster gathered samples belonging in majority to spring or summer and (a) to the biggest patches (Very-large), or to (b-c) the other treatments (Large to Bare); although this second cluster may be divided into two, i.e. (b) intermediate size of patches (Large to Small) and (c) smallest patches and all bare samples. Then, three other clusters gathered samples belonging in majority to fall (and somewhat summer) and respectively to d) largest patches of forests (Very-large to medium), e) intermediate sizes (large to small) and f) the bare treatment samples alone.

For both experiments, the separation between samples of different treatments (Fig. 10b) was correlated to densities of *Symphodus* spp. (ss), *Muraeana helena* (mh), *Serranus* spp. (se) and *Scorpaena porcus (*po); and inversely to densities of *Mullus* (mu) and crypto-benthic (bg) juveniles. Distinction of samples according to months and seasons was correlated to densities of *Symphodus cinereus* (ci) and *Coris julis* (cj) and inversely to densities of *Diplodus vulgaris* (dv) and *D. sargus* (ds).

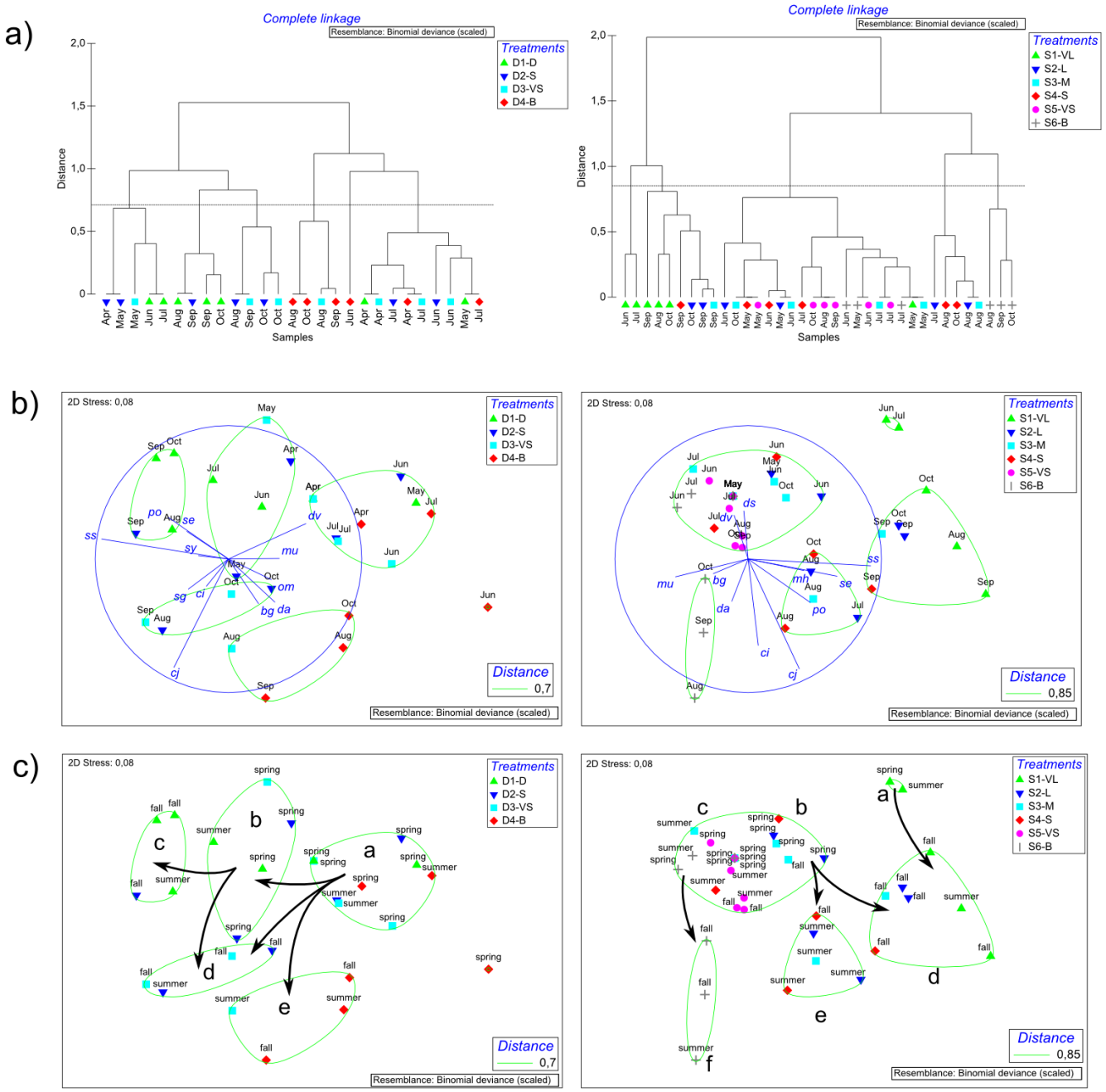


Fig. 10. Graphical representations of juvenile assemblage's composition according to patch-density and patch-size treatments and months. a: Dendograms, dashed lines figure the distance (dissimilarities) at which slicing was done. b&c : nMDS plots for patch-density (left) and patch-size (right) treatments: figuring centroids of treatment replicates for each levels of factors months and treatments; 2D stress (0.08) is good; thin green circles figure clusters given by slicing dendograms at indicated distance; Panel c shows months expressed as season as a visual aid (see M&M for details) as well as black arrows displaying trajectories of each treatment along seasons ; lowercase characters as referred to into the text.

- Juvenile assemblage composition : multivariate inferential approach

In 2010 interaction term between months and patch-density treatments was significant (PERMANOVA, F = 2.6, p = 0.0061) i.e. density-treatments effect on juvenile assemblage was different according to months (Fig. 12a) : in April and May assemblages did not differ between the four treatment (pair-wise tests, p > 0.1) although this was probably due to a low number of replicates ; in June and July, assemblage on « dense » treatment significantly differed from sparse, very-sparse and bare treatments (in June: pair-wise tests, respectively p = 0.095, 0.039, 0.025 ; and in July: pair-wise tests, respectively p = 0.083, 0.053, 0.029). These last three treatments did not differ from each other (pair-wise tests, p> 0.1). In August, assemblages did not differ between dense, sparse and very-sparse treatments (pair-wise tests, p> 0.1), however each of these differed from bare treatment (see Fig. 12a, pair-wise tests, respectively p = 0.027, 0.013, 0.079). In September, D treatment assemblage differed from VS, but not from S. Besides D, S and VS differed from bare treatment (pair-wise tests, respectively p = 0.007, 0.033, 0.020). Finally, in October, D treatment assemblage differed from others treatments (pair-wise tests, respectively p = 0.029, 0.035, 0.060) and no significant differences appeared among them.

In 2011 interaction term between months and patch-size treatments was not significant (PERMANOVA, F = 0.96, p = 0.540) but months term and treatments term were both significant (PERMANOVA, F = 7.51 and 11.31; both p < 0.001), i.e. size-treatments effect on juvenile assemblage was constant through months and vice-versa. Assemblages differed significantly between all patch-size treatments (PERMANOVA, see Fig. 11a for pairwise test results), except between medium and small, and between medium and very-small (pair-wise tests, respectively p = 0.605 and 0.218). For the factor months (Fig. 11b), assemblages did not differ (pair-wise tests, p > 0.1) between closed-by months i.e. between May-June-July, between September-October, while August assemblage differed from all the others. July assemblage did not differed from September and October ones (Fig. 11b).

For both experiment, as revealed by the PERMANOVA, juvenile assemblages evolved through months and seasons. But each season, the effect of treatments was visible. By analyzing the barplot (Fig. 11a) and correlation vectors (Fig. 10b) we deduce that assemblage evolution through time was mainly correlated to an increase of *Coris julis* and *Symphodus cinereus* juvenile densities, and a decrease of *D. vulgaris* and *D. sargus* juvenile densities, for all treatments. On the other hand, at each season, both patch-size and patch-density reduction was associated to a reduction of *Symphodus* spp., *Serranus* spp., *M. helena* and *S. porcus* juvenile densities, as well as to an increase of *Mullus* and crypto-benthic juvenile densities.

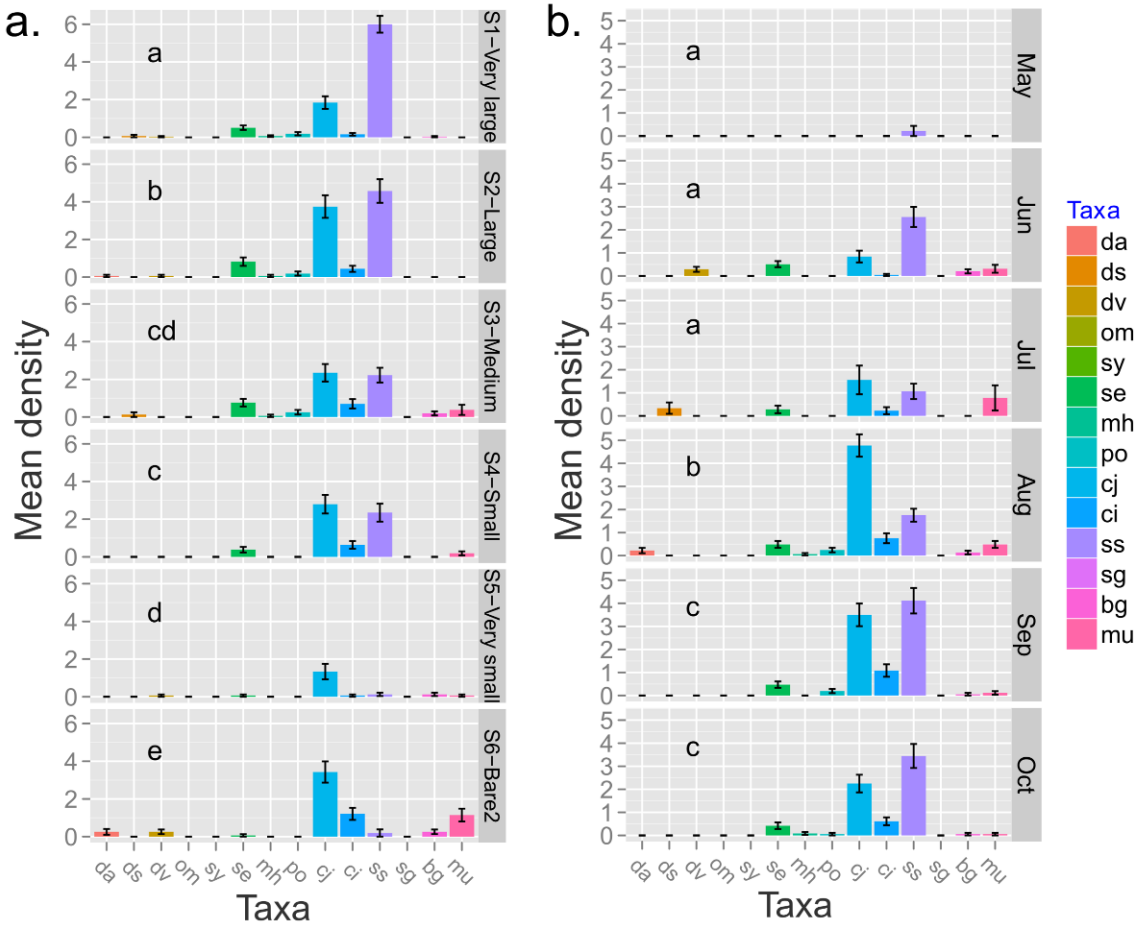


Fig. 11a: Patch-size experiment - juvenile densities for each treatment averaged over the full year, per taxa – error bares = s.e. - –pairwise tests between treatments are given (different lower case characters indicate significant differences between treatments)

Fig. 11b: Patch-size experiment - juvenile densities per taxa for each month averaged over all treatments - – pairwise tests between months are given (different lower case characters indicate significant differences between months)

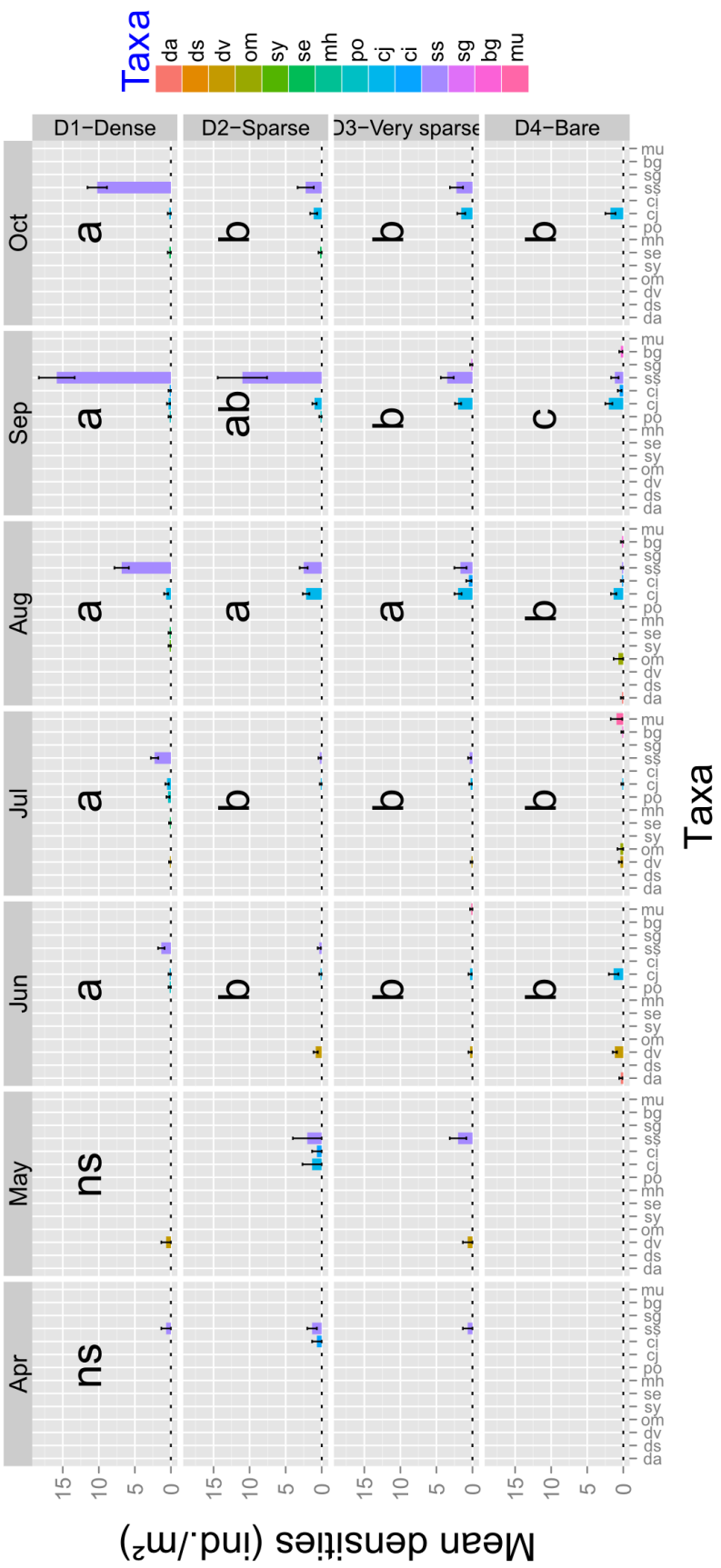


Fig. 12: Patch-density experiment - juvenile densities for each treatment–replicates averaged over each month, per species – for a given month, pairwise tests between treatments are given (different lower case characters indicate significant differences between treatments)

Juvenile assemblage composition : univariate inferential approach

- Species richness

For the patch-density experiment (2010), when looking at species richness per census and per treatment, interaction term between month and density-treatments was significant (PERANOVA, $F = 2.21$, $p = 0.005$) : census species richness averaged by month differed between treatments and differences evolved through months without an obvious pattern (Fig. 13, see pair-wise tests results therein). Besides, treatment term alone was not significant but month term was (PERANOVA, $F = 8.35$, $p < 0.001$) : i.e. richness per census, averaged over all treatments and by month, differed according to months and reached a maximum in September (Fig. 13 and pairwise tests results therein).

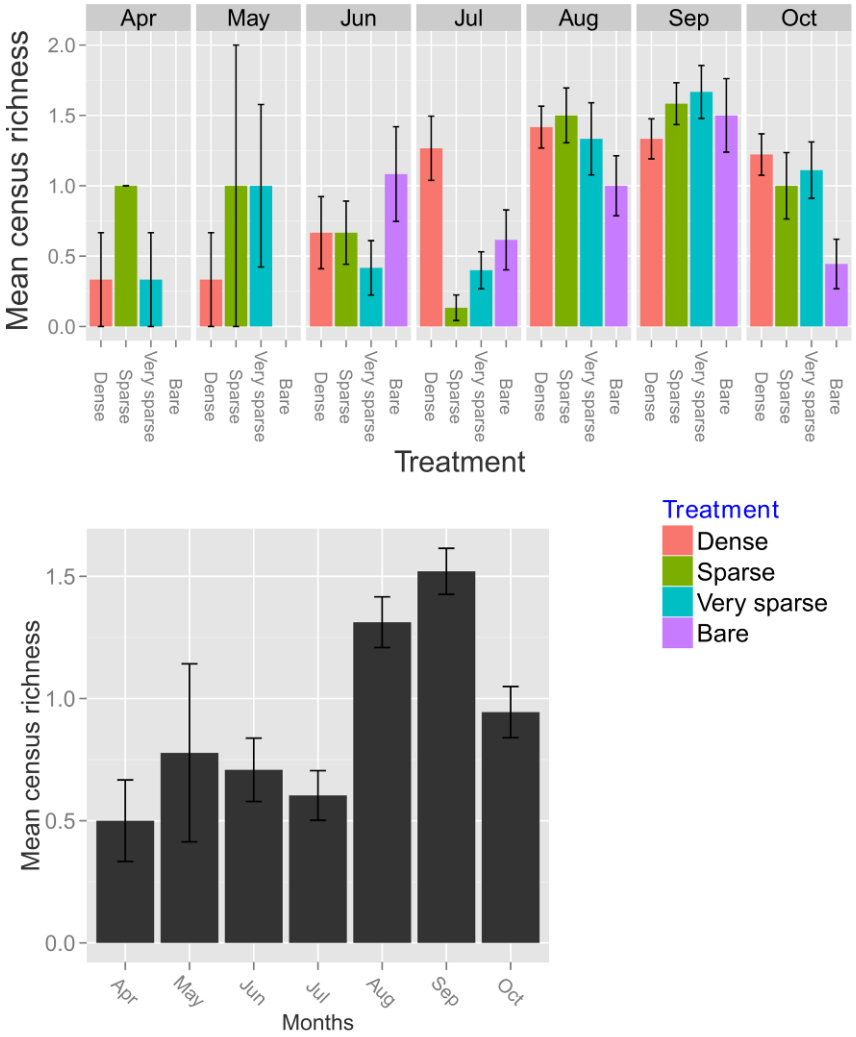


Fig. 13. Patch-density experiment - richness per treatment and per censuses - error bares = s.e.

For the patch-size experiment (2011), when looking at species richness per census and per treatment, interaction term between month and size-treatments was significant (PERANOVA, $F = 1.76$, $p = 0.014$) : census species richness averaged by month differed between treatments and differences evolved through months (see pair-wise tests results on Fig. 14). Besides, treatment term and month term were both significant (PERANOVA, respectively $F = 13.44$, $p < 0.001$ and $F = 18.38$, $p < 0.001$) : i.e. richness per census averaged over the full year differed between treatments and richness per census averaged over all treatments differed between months (Fig. 14). It is worth noting that for each month, and also for the treatment term alone, census richness tended to decrease as patch-size decreased. For the month term alone, census richness tended to increase through months to reach a maximum in September (Fig. 14).

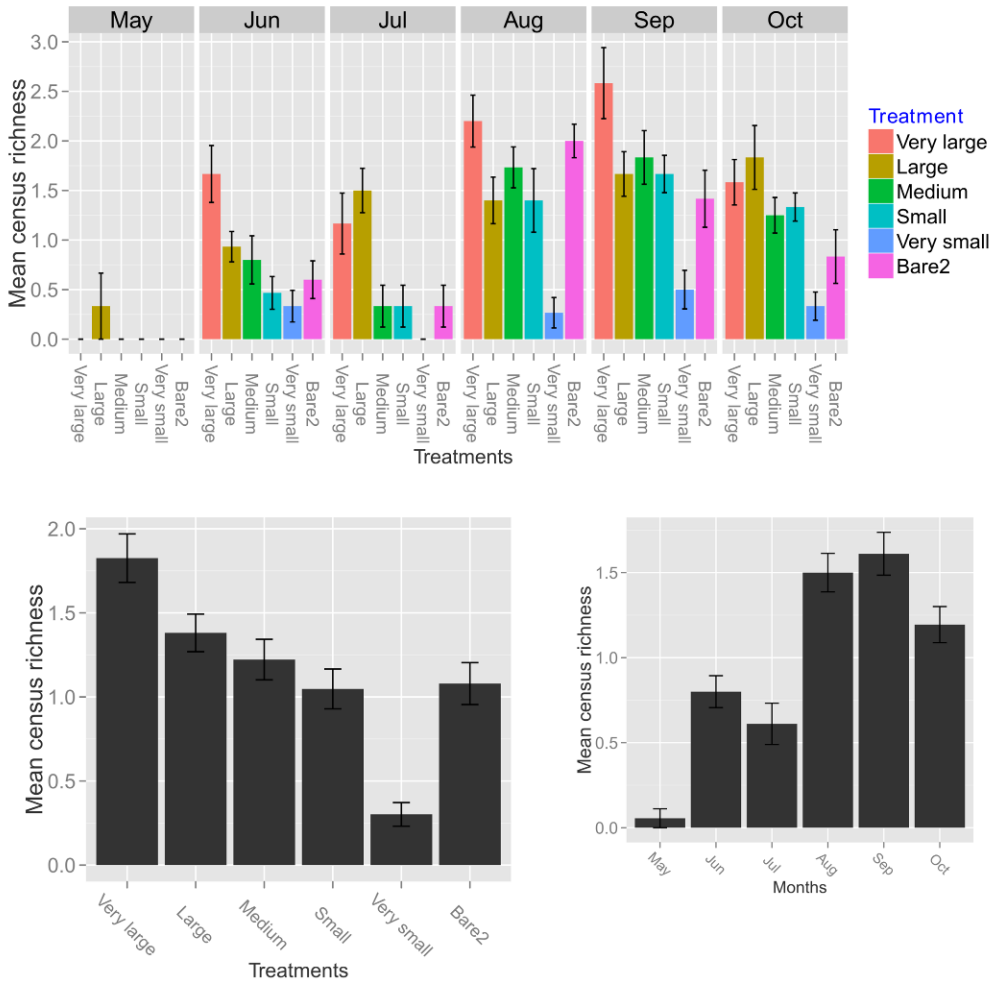


Fig. 14 Patch-size experiment - richness per treatment and per censuses - error bares = s.e.

In 2010, the species richness cumulated over the full year (annually cumulated richness per treatment) did not differ between patch-density treatments, whereas in 2011 it differed significantly between patch-size treatments (Fig. 15; PERANOVAs, respectively $F = 2.8$, $p = 0.107$ and $F = 4.24$, $p = 0.020$). Very-large patches displayed the highest annual richness (9.0 ± 0.6 (se)), very-small patches displayed the lowest (3.3 ± 1.5 (se)) while other treatments displayed intermediate levels of richness.

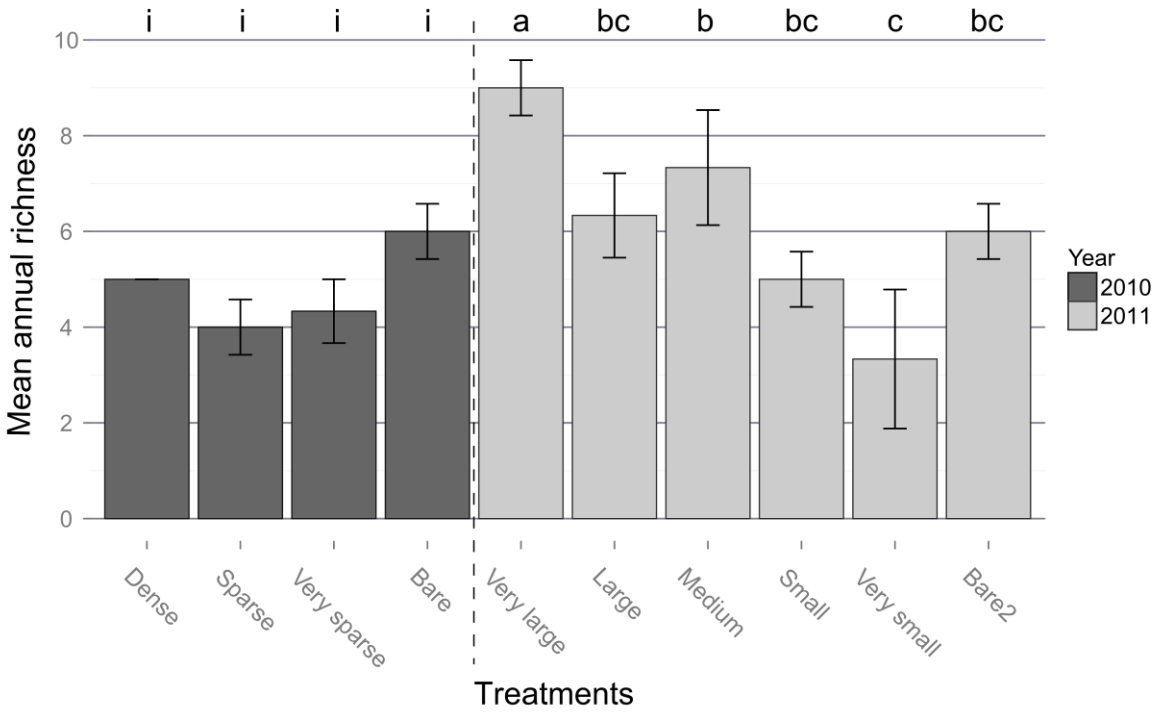


Fig 15. Mean annually cumulated richness per treatment – error bares = s.e. – for a given year, between-treatments comparisons (pairwise tests results) are given (different lower case characters indicate significant differences between treatments)

- Total density (all species)

Patch-density experiment (2010)

When studying total abundance of all species together, during the patch-density experiment (2010), both interaction terms between census and treatments and between months and treatments were significant (Fig 16a and Fig. 17; PERANOVAs, respectively $F = 1.54$, $p = 0.030$ and $F = 3.75$, $p = 0.002$). Over 22 censuses, 13 censuses (3/5) displayed significant differences between density-treatments. Moreover, no differences appeared during the "spring" month censuses (April to June), 2/3 of "summer" censuses (July-August) displayed differences between treatments, while 100% of "fall" censuses (September-October) displayed significant differences. Out of the 13 censuses displaying differences, 12 censuses displayed a pattern of juvenile density such as [D]>[S and/or VS and/or B] ; besides, in 5

cases (i.e. about 1/4 of all censuses) and also when looking at the treatment term alone (PERANOVA, F = 6.04, p = 0.007) the significant pattern was such as [D]>[S]>[VS] (Fig. 16b). Pair wise comparisons for the months-treatments interaction displayed similar patterns (Fig. 17).

When performing pairwise comparisons between pairs of months, D, S and VS treatments displayed the same rough pattern i.e. summer-fall months displayed higher densities of juveniles than spring and early summer months (Fig 18a+b and pairwise tests results therein).

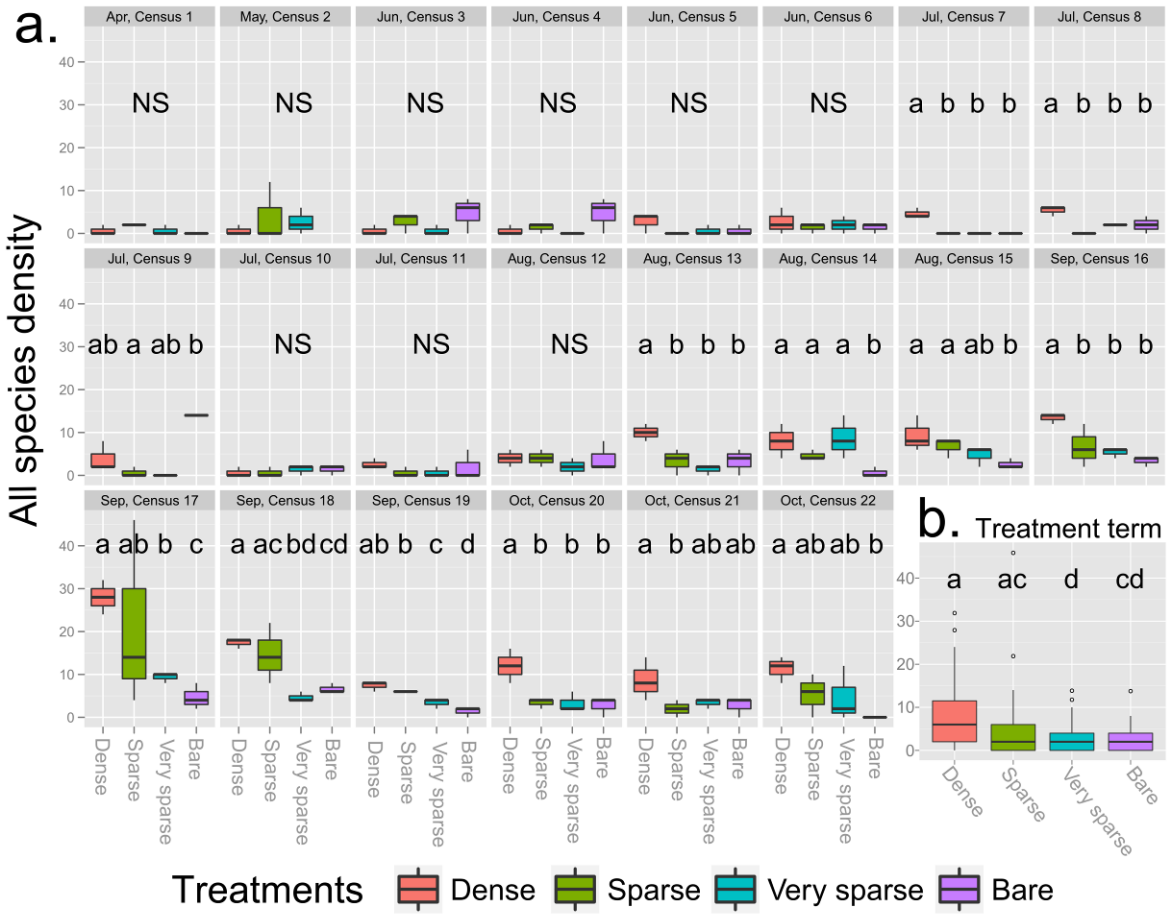


Fig. 16. All-species juvenile density per census and per density-treatment (2010) – a: Tuckey boxplots of juvenile densities (ind. m^{-2}) per treatments and per weekly censuses from April to October 2010; For each censuses, between-treatment comparisons (pairwise tests results) are given (different lower case characters indicate significant differences) ; b: for the treatment term alone.

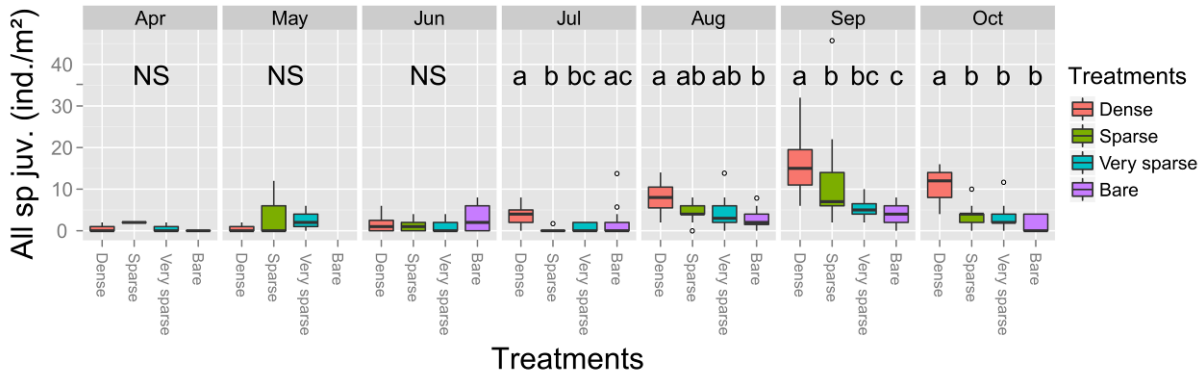


Fig. 17– Tuckey boxplots of juvenile densities (all species, ind. m^{-2}) per treatment and by month from April to October 2010; between-treatments comparisons (pairwise tests results) are given (different lower case characters indicate significant differences between treatments)

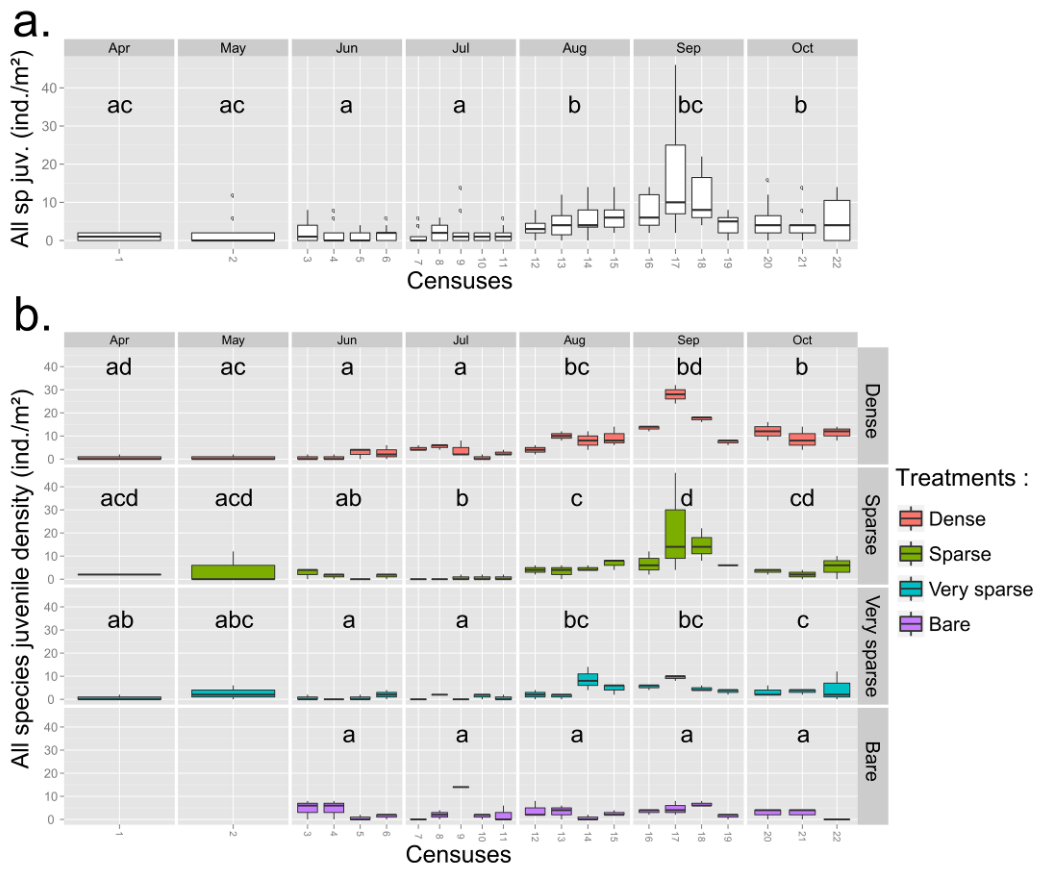


Fig. 18 – Tuckey boxplots of juvenile densities (all species, ind. m^{-2}) per census and by month from April to October 2010; between-month comparisons (pairwise tests results) are given (different lower case characters indicate significant differences between months) – a: all treatment confounded ; b: according to density-treatment (2010)

Patch-size experiment (2011)

During the patch-size experiment interaction term between census and treatment was not significant but interaction term between month and size-treatment was (Fig. 19; PERANOVAs, respectively $F = 1.05$, $p = 0.373$ and $F = 2.21$, $p = 0.005$). In May (only one census) no significant differences appeared between treatments. From June to October, the smaller size treatment (VS) displayed systematically lower juvenile densities than larger treatments (VL to S). Besides, if looking at the treatment term alone (Fig. 19b), juvenile density was the highest in the very large treatment [VL] and decreased as patch-size decreased, such as [VL]=[L]>[M]=[S]>[VS], while Bare treatment (B) had an intermediate position, not different from Medium and Small treatments (see Fig. 19b for pairwise tests details). When comparing pairs of levels for the month factor over all treatments, or separately for each treatment except the very-small (VS), juvenile density tended to increase through time with a maximum in August-September (Fig. 19c and pairwise tests results therein).

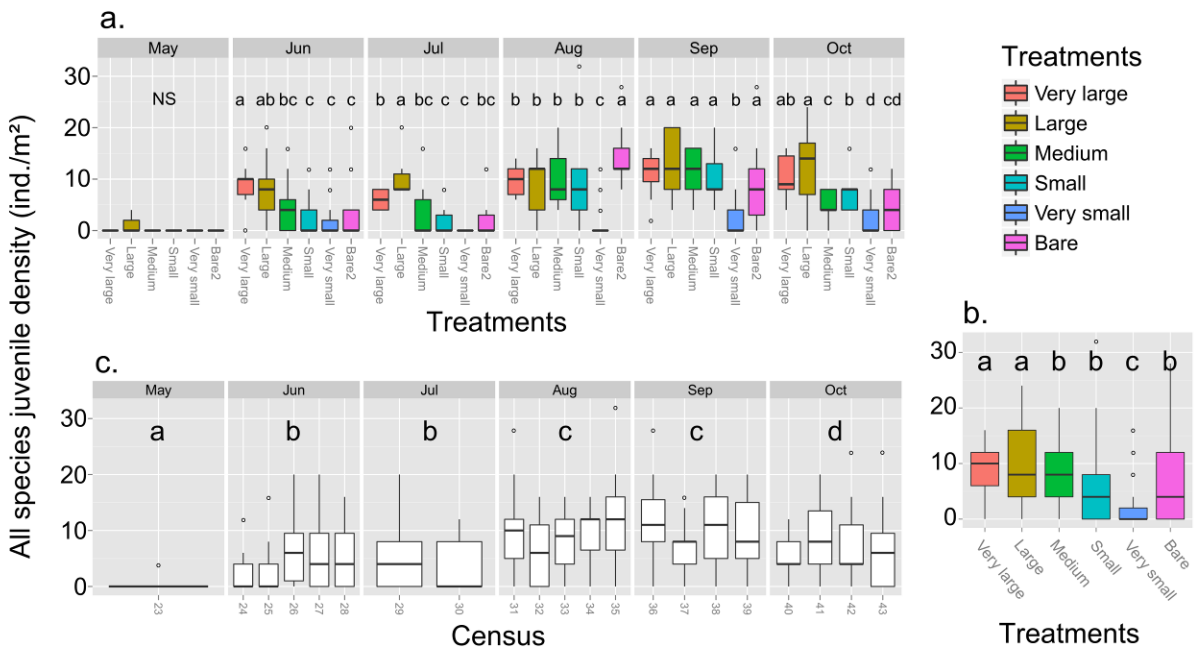


Fig. 19– a: Tuckey boxplots of total juvenile densities (all species, ind. m^{-2}) per patch-size treatments and by months from May to October 2011; pairwise tests results are given (different lower case characters indicate significant differences) ; b: pairwise comparisons between treatment-factor levels ; c : pairwise comparisons between month-factor levels

Taxa-specific effect of patch-density and patch-size

Taxa-specific patterns of abundances (total and per size-class)

When considering taxa-specific densities, for both patch-density and patch-size experiments, interaction term between taxa and treatments was significant (PERANOVA, both $p < 0.01$). Consequently, for the most frequent taxa, we present below our results taxa by taxa.

- *Symphodus* spp.

During the patch-density experiment, over the full 2010 year, “dense” treatments displayed the highest *Symphodus* spp. juvenile densities (6.3 ± 0.9 (SE) ind. m^{-2}, treatment term, PERANOVA, $F = 13.62$, $p < 0.001$), which decreased in sparser treatments so that [D] > [S] = [VS] > [B] (see pair-wise tests, Fig. 20a). Besides, both interaction terms between censuses and patch-density treatment and between months and patch-density treatment were significant (PERANOVA, respectively $F = 1.47$, $p = 0.043$ and $F = 4.81$, $p < 0.001$). Over the 22 censuses from April to October 2010 (Fig. 21), no differences between treatments appeared during the April to June censuses, although in June, when present, juveniles were observed only on dense or sparse treatments. In July, during the three first censuses (over five), “dense” treatments displayed significantly higher densities of juvenile; from the second census of August until end of October (10 censuses), dense treatment systematically displayed significantly higher densities of juveniles, while for half of these censuses others treatments displayed a juvenile density pattern such as [S] > [VS] > [B] (pair-wise tests, Fig. 21).

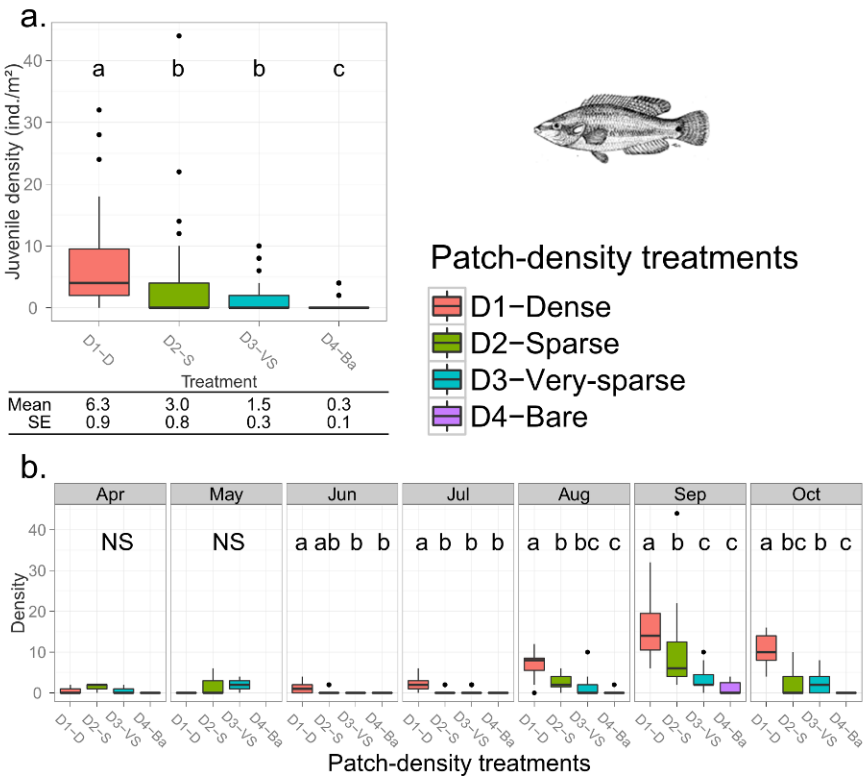


Fig. 20 – Tuckey boxplots of total *Symphodus* spp. juvenile densities (ind. m^{-2}) per patch-density treatments (a) and by months from April to October 2010 (b); pairwise tests results are given (different lower case characters indicate significant differences between treatments)

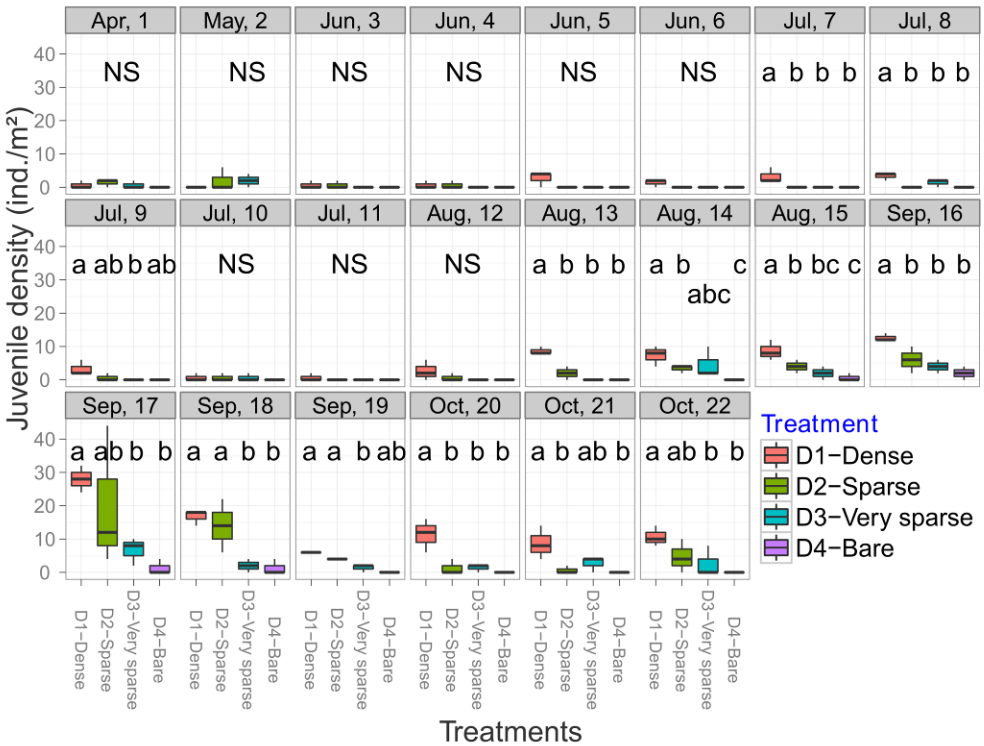


Fig. 21 – Tuckey boxplots of total *Symphodus* spp. juvenile densities (ind. m^{-2}) per patch-density treatments and by census (arabic numerals) from April to October 2010; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

During the patch-size experiment (2011), *Symphodus* spp. juveniles densities decreased as the patch-size was decreasing (treatment term, PERANOVA, $F = 18.94$, $p < 0.001$), so that [VL] = [L] > [M] = [S] > [VS] = [B] (Fig. 22a and pair-wise tests therein). Interaction term between months and treatments was slightly significant and the same pattern of juvenile density among treatments occurred each months except in May where only few individuals were observed (Fig. 22b and pair-wise test therein).

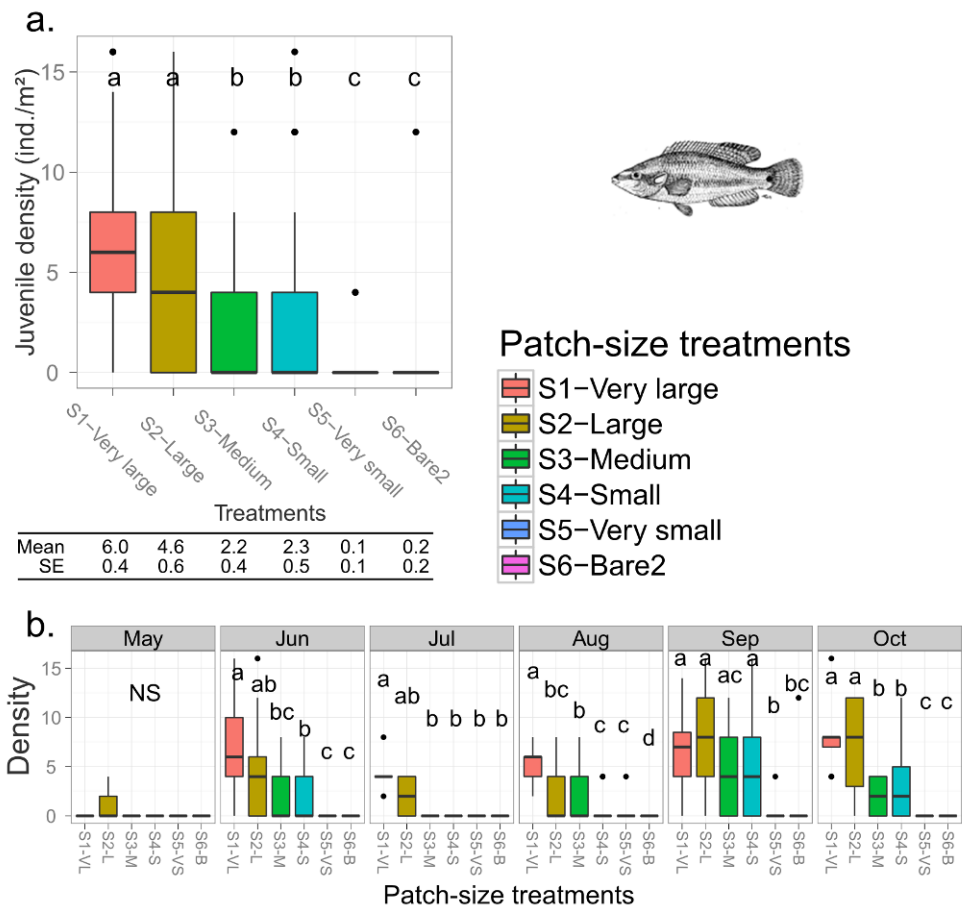


Fig. 22– Tuckey boxplots of total *Symphodus* spp. juvenile densities (ind. m^{-2}) per patch-size treatments (a) and by months from May to October 2011 (b); pairwise tests results are given (different lower case characters indicate significant differences between treatments)

For *Symphodus* spp., for both experiments, interaction term between size-class and treatment was significant (PERANOVAs, respectively $F = 6.59$, $p < 0.001$ and $F = 2.69$, $p = 0.016$). During the patch-density experiment (2010), "small" *Symphodus* spp. juveniles displayed significantly higher mean densities in "dense" patches (1.9 ± 0.3 (SE) ind. m^{-2}) than in sparser or bare treatments, which didn't differ among themselves (pair-wise tests, Fig. 23a). Similarly, "small" *Symphodus* spp. juveniles displayed higher mean densities in "very-large" and "large" patches (respectively 1.8 ± 0.3 (SE) and 1.4 ± 0.4 (SE) ind. m^{-2}) than

in smaller or bare treatments, which didn't differ among themselves (pair-wise tests, Fig. 23b). For both experiments, "medium" and "large" juveniles displayed similar patterns of densities among levels of treatments, but differences between treatment levels were less sharp : intermediate levels of treatments (i.e. respectively "sparse" and "very-sparse" and "large" to "small" displayed intermediate densities of juveniles (Fig. 23a+b).

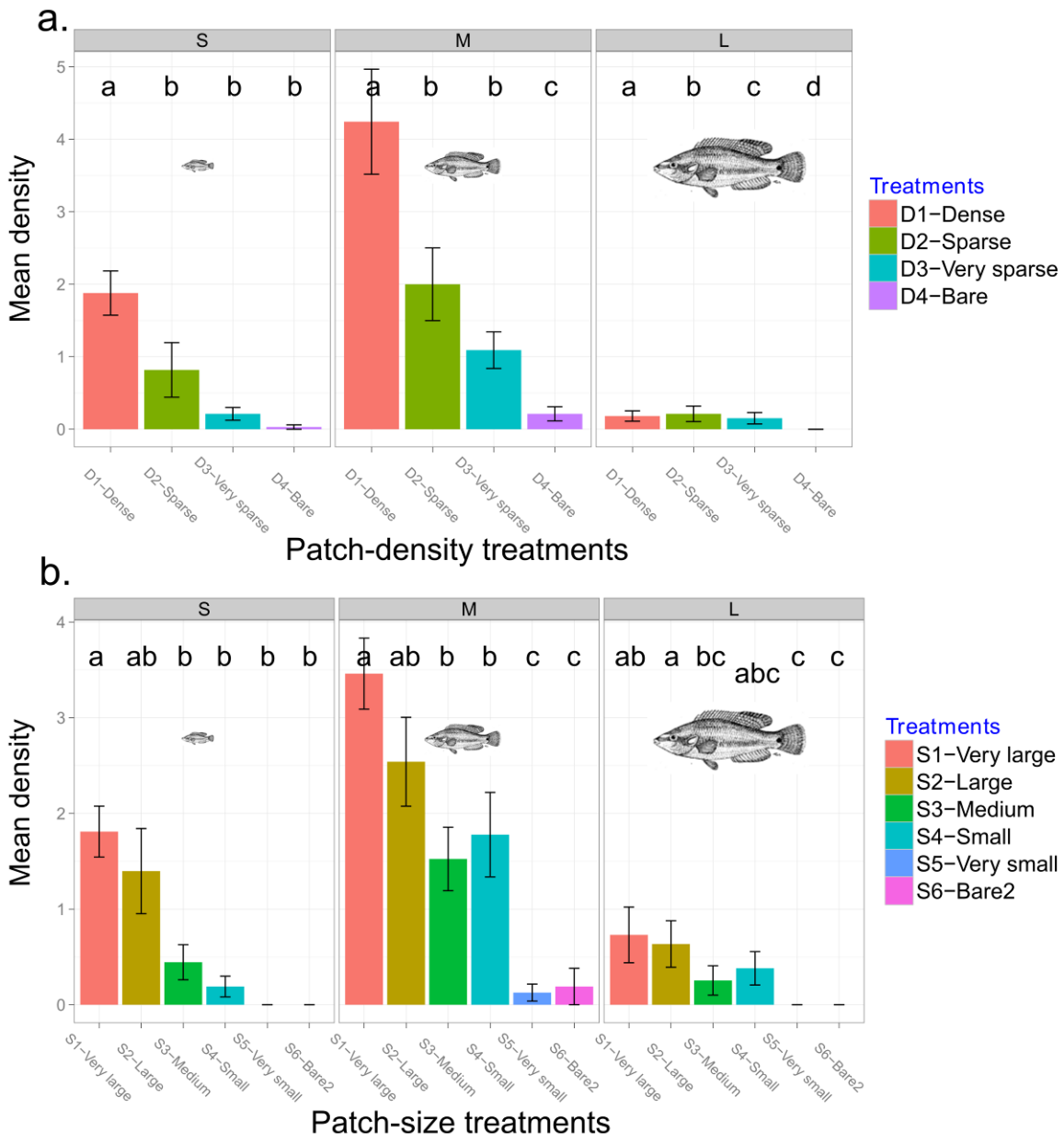


Fig. 23 – *Symphodus* spp. juvenile mean (±se) densities (ind. m^{-2}) per size-classes and per treatments: patch-density experiments (a) and patch-size experiments (b) ; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

- *Symphodus cinereus*

In 2010 during the patch-density experiment, few individuals were observed in the experimental area (mean densities of 0 to 0.5 ind. m^{-2} per census) and no significant differences appeared between treatments (PERANOVA, F = 1.52, p = 0.223). During the patch-size experiment, treatment terms was slightly significant (PERANOVA, F = 2.14, p = 0.081): over the full 2011 year, bare treatment displayed the highest mean of *S. cinereus* densities (1.2 ± 0.3 (SE) ind. m^{-2}), while very-small and very large patches displayed the lowest densities (pair-wise tests, Fig. 24). Interaction term between size-class and treatment was not significant (PERANOVA, F = 1.06, p = 0.346).

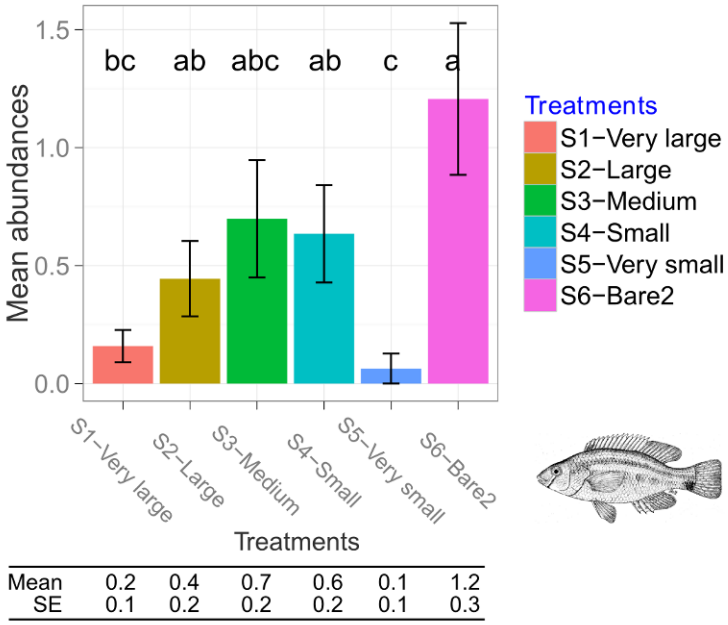


Fig. 24– patch-size experiment : *Symphodus cinereus*. juvenile mean densities (ind. m^{-2}) per treatments ; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

- *Coris julis*

During the patch-density experiment, over the full 2010 year, “dense” treatments displayed the lowest *Coris julis* juvenile densities (0.4 ± 0.1 (SE) ind. m^{-2}, treatment term, PERANOVA, F = 2.80, p = 0.050), which increased in sparser treatments so that [D] < [S] = [VS] = [B] (see pair-wise tests, Fig. 25a). Interaction terms between censuses and patch-density treatment and between months and patch-density treatment were not significant (PERANOVA, respectively F = 1.07, p = 0.356 and F = 1.61, p = 0.105). During the patch-size experiment, over the full 2011 year, “large” and “bare” treatments displayed the highest *Coris julis* juvenile densities (respectively 3.7 ± 0.6 (SE) ind. m^{-2} and 3.4 ± 0.6 (SE) ind. m^{-2}), “very-large, medium and small” patch-size treatments displayed intermediate juvenile densities, while “very-small” treatment displayed the smallest *Coris* densities (1.3 ± 0.4 (SE) ind. m^{-2}) (treatment term, PERANOVA, F = 3.47, p = 0.007, see pair-wise tests, Fig. 25b). Interaction term between months and patch-size treatments was significant (PERANOVA, F = 2.02, p = 0.013, Fig. 25c) : the previous pattern was approximately observed each month from June to October, while in May no individuals were observed.

During both experiments, although more significantly for patch-density experiment, interaction term between month, treatment and size-class was significant (PERANOVA, respectively F = 1.99, p = 0.006 and F = 1.47, p = 0.058): in 2010 (patch-density experiment) “large” individuals, for each month, tended to be more numerous in very-sparse and bare plots, while “small-medium” juveniles, at settlement (in August) tended to be more numerous in sparse and very-sparse treatments, before to switch towards bare plots in September (pairwise tests, Fig 26).

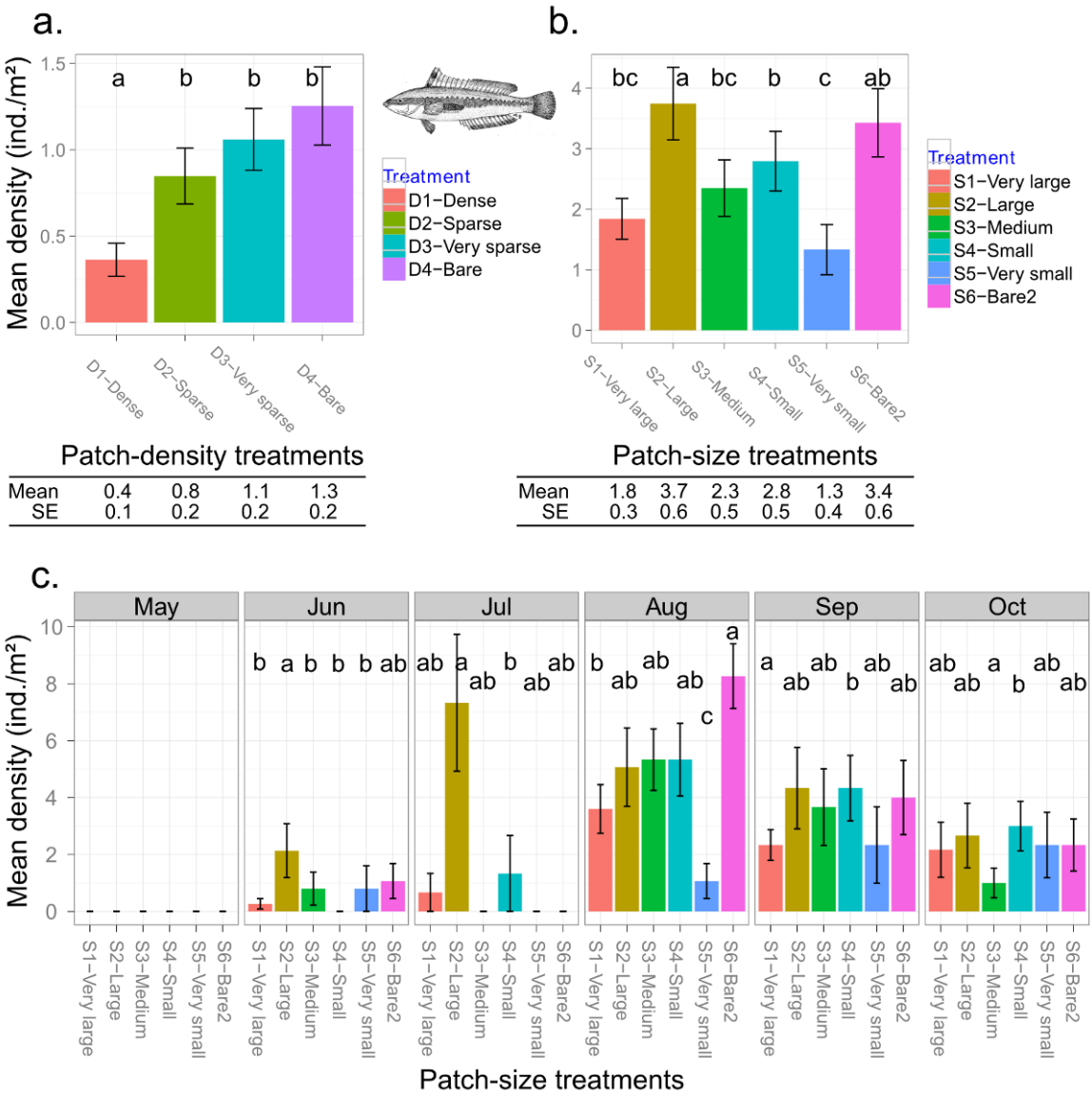


Fig. 25 – *Coris julis* juvenile mean densities (ind. m^{-2}) per treatments (patch-density (a) and patch-size (b) experiments) and through months for 2011 (c) ; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

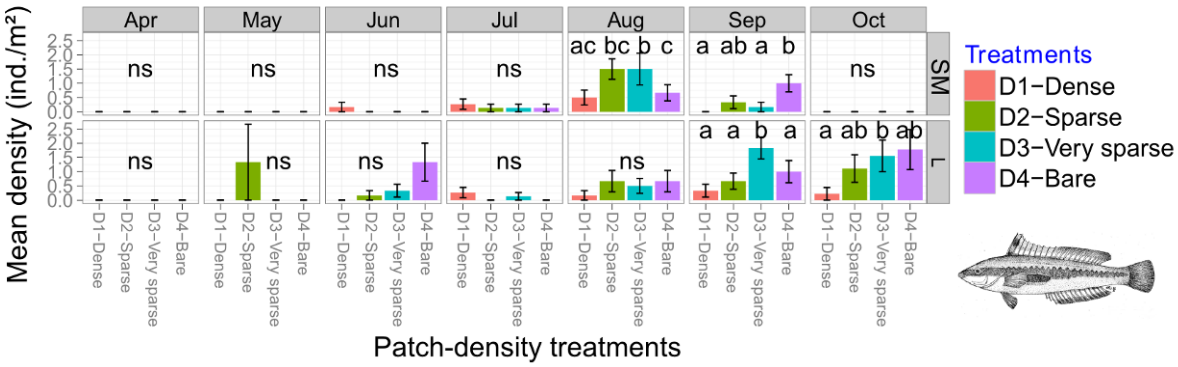


Fig. 26 – *Coris julis* juvenile mean densities (ind. m^{-2}) by size-classes (small-medium, large), per patch-density treatments and through months for 2010 ; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

- *Serranus* spp.

During the patch-density experiment (2010) few individuals only (n = 4) were observed and no significant differences appeared between treatments, however, when present, *Serranus* juveniles were seen only on dense and sparse treatment, never on very-sparse or bare substratum. During the patch-size experiment (2011) the treatment term and census term only where significant (PERANOVA, respectively F = 2.87, p = 0.021 and F = 2.48, p = 0.003): "large" patches (L) displayed the highest *Serranus* spp. mean densities (0.8 ± 0.2 (se) ind. m^{-2}) and smaller patches displayed decreasing mean densities (pair-wise tests, see Fig. 27). Interaction term between size-class and treatment was not significant (PERANOVA, F = 2.87, p = 0.021).

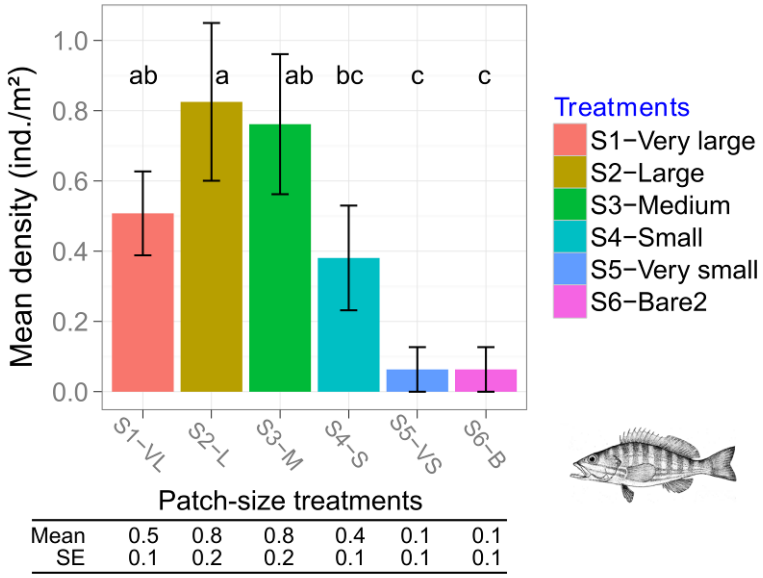


Fig. 27 – patch-size experiment : *Serranus* spp. juvenile mean densities (ind. m^{-2}) per treatments ; pairwise tests results are given (different lower case characters indicate significant differences between treatments)

- *Scorpaena porcus* and *Muraena helena*

For *Scorpaena porcus* few individuals were observed and no significant differences appeared between both patch-density and patch-size treatments (PERANOVA, respectively F = 0.91, p = 0.398 and F = 1.40, p = 0.244). However, when present, individuals were only observed on denser (dense and sparse) and larger (very-large to medium) treatments. *Muraena helena* individuals displayed the same pattern for patch-size treatments while densities in 2010 were too low to allow us to make conclusions for the patch-density effect.

Taxa-specific effect of treatment on total length (TL) and behavior of juveniles

- *Symphodus* spp.

For *Symphodus* spp., proportion of juvenile behaviors varied according to treatments (Fig. 28a+c) but varied also according to TL (Fig. 28b+d). Besides, mean total length of juveniles (TL) differed significantly between both patch-density and patch-size treatments (PERANOVAs, respectively $F = 4.41$, $p = 0.006$ and $F = 1.94$, $p = 0.084$): length of juveniles tended to increase in sparser and smaller patches (pair-wise tests, Fig. 29).
As a consequence, for further analysis we had to be careful not to confound effect of size-class (SC) and effect of treatment on behavior and we consequently decided to analyze the effect of treatments on behaviors separately per SC : during the patch-density experiment, for small, medium and large size-classes interaction term between behavior and treatment was significant (PERANOVAs, $p<0.1$; Fig. 30a and pairwise tests results therein); for both small and medium juveniles, in the “dense” treatments, juveniles were significantly more “permanent” than “temporary”; contrastingly, in sparser treatments their behavior became more “temporary”. During the patch-size experiment a similar effect was observed: small juveniles were exclusively cryptic or deambulatory in very-large to medium patches, and absent in smaller patches. Medium juveniles were mainly deambulatory in very-large to medium patches and tended to become more temporary in small patches; large juveniles were mostly temporary (Fig. 30b and pairwise tests results therein).

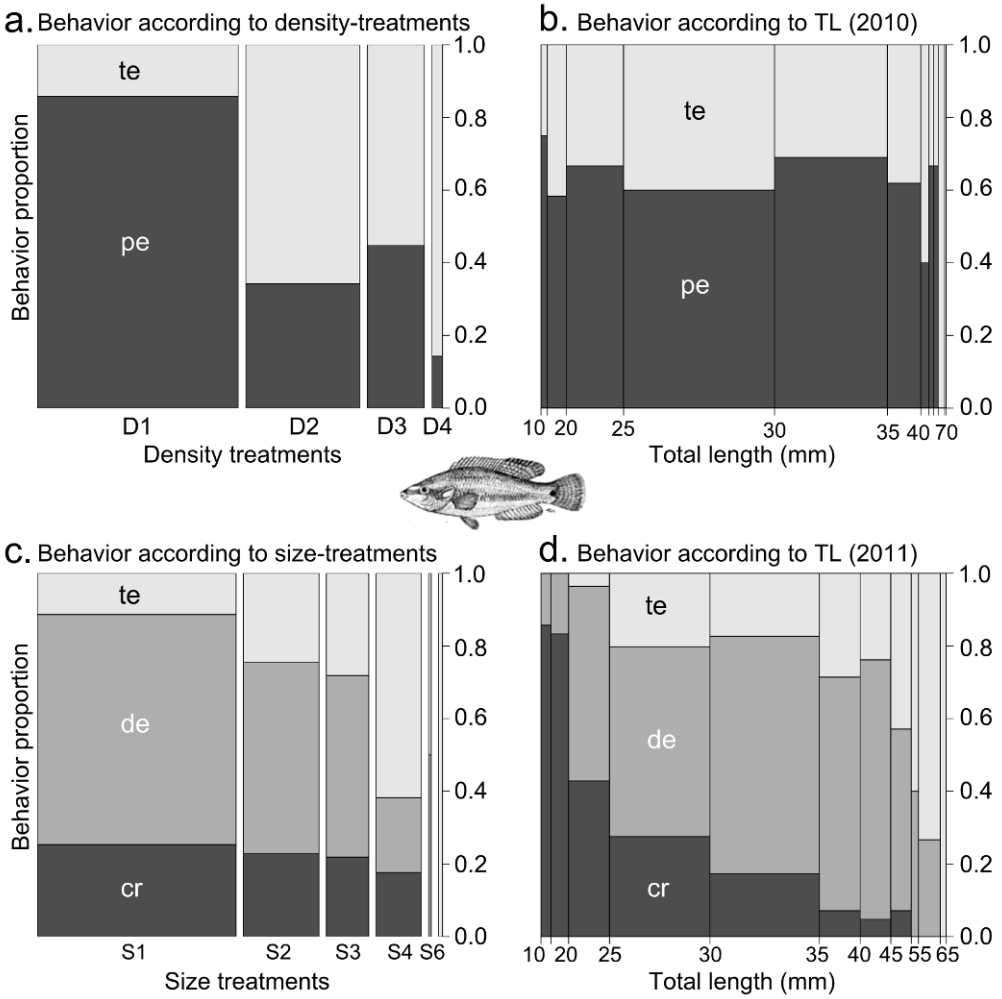


Fig. 28 : *Symphodus* spp. juveniles behavior according to patch-density (a) and patch-size (c) treatments and according to 2010 (b) and 2011 (d) individuals total length (TL, mm); Behavior: cr = cryptic, de = deambulatory, pe = permanent, te = temporary ; bares-width proportional to juvenile abundances per treatment or TL levels.

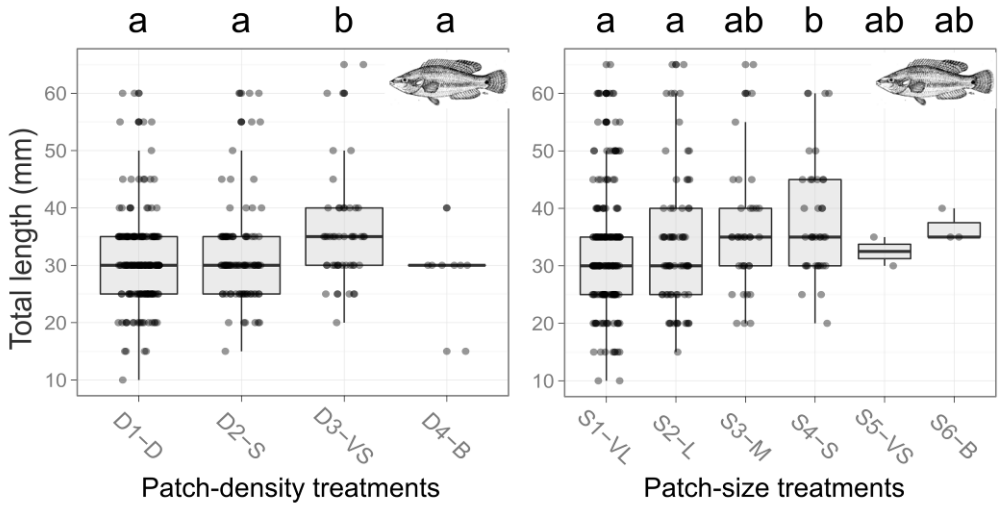


Fig. 29 : Tuckey boxplots superimposed with stripchart of *Symphodus* spp. juveniles total length (TL, mm) per treatments ; pairwise tests results are given (for a given experiment, different lower case characters indicate significant differences between treatments)

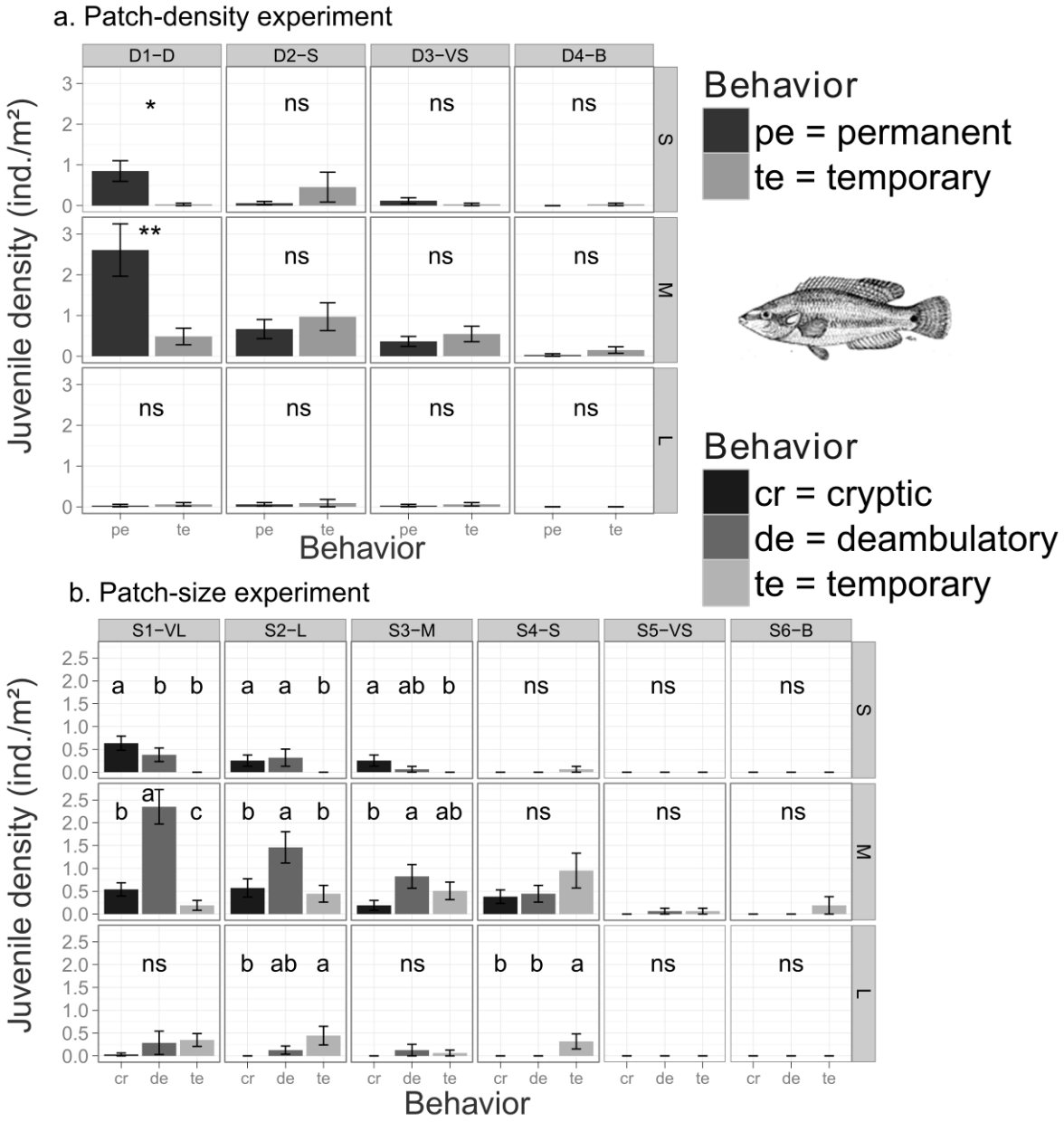


Fig.30. *Symphodus* spp. juveniles densities per behavior, according to size classes and patch-density (a) or patch-size (b) treatments; Behavior: cr = cryptic, de = deambulatory, pe = permanent, te = temporary ; pairwise tests results are shown (for a given size-class, for a given treatment, different lower case characters or asterisk indicate significant differences between behaviors).

- *Symphodus cinereus*, *Serranus* spp., *Coris julis*

Analysis of the effects of treatments on behavior for these taxa will be included in the submitted version of the paper.

Forest fragmentation effects tested in natural habitats

Natural habitats characteristic, observed species and size ranges

In early August 2010, within the studied natural habitats next to Garganellu islet (Fig. 1), wide forest and patches of *Cystoseira balearica* displayed canopies characterized by a mean canopy height about 15 cm (respectively 16.7 ± 0.4 (se) and 14.8 ± 0.4 (se) cm) and a mean percent coverage above 95 % (Fig. 31). Wide bush-land and patches of Dictyotales and Sphacelariales (DS) were characterized by a mean DS canopy height about 5 cm (respectively 6.2 ± 0.3 (se) and 4.3 ± 0.1 (se) cm) and a mean DS percent coverage between 50 and 90 % (Fig. 31).

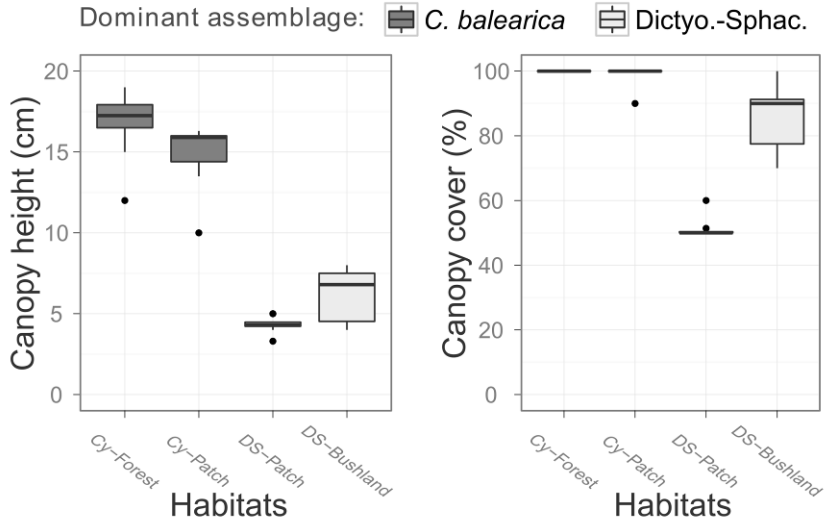


Fig. 31. Canopy height and percent cover of dominant assemblage in each studied habitats

All habitats pooled, only 3 frequent juvenile taxa were observed during our censuses: *Symphodus* spp. (i.e. S. *ocellatus*, *S. roissali* and *S. tinca*) were significantly more numerous than *Coris julis* juveniles and than Blenniidae-Gobiidae-Tripterygiidae juveniles which displayed the lowest observed densities (Fig. 32, PERANOVA: $F = 29.11$, $P < 0.001$). *Symphodus* spp. juvenile size distribution displayed a mode at 20 mm TL, while *C. julis* individuals' sizes were about 30 mm TL. The third taxa did not display a clear mode in its size distribution (Fig. 32a). A single *Serranus cabrilla* was censused over the entire study area. Consequently further analysis only focused on the previous three frequent taxa.

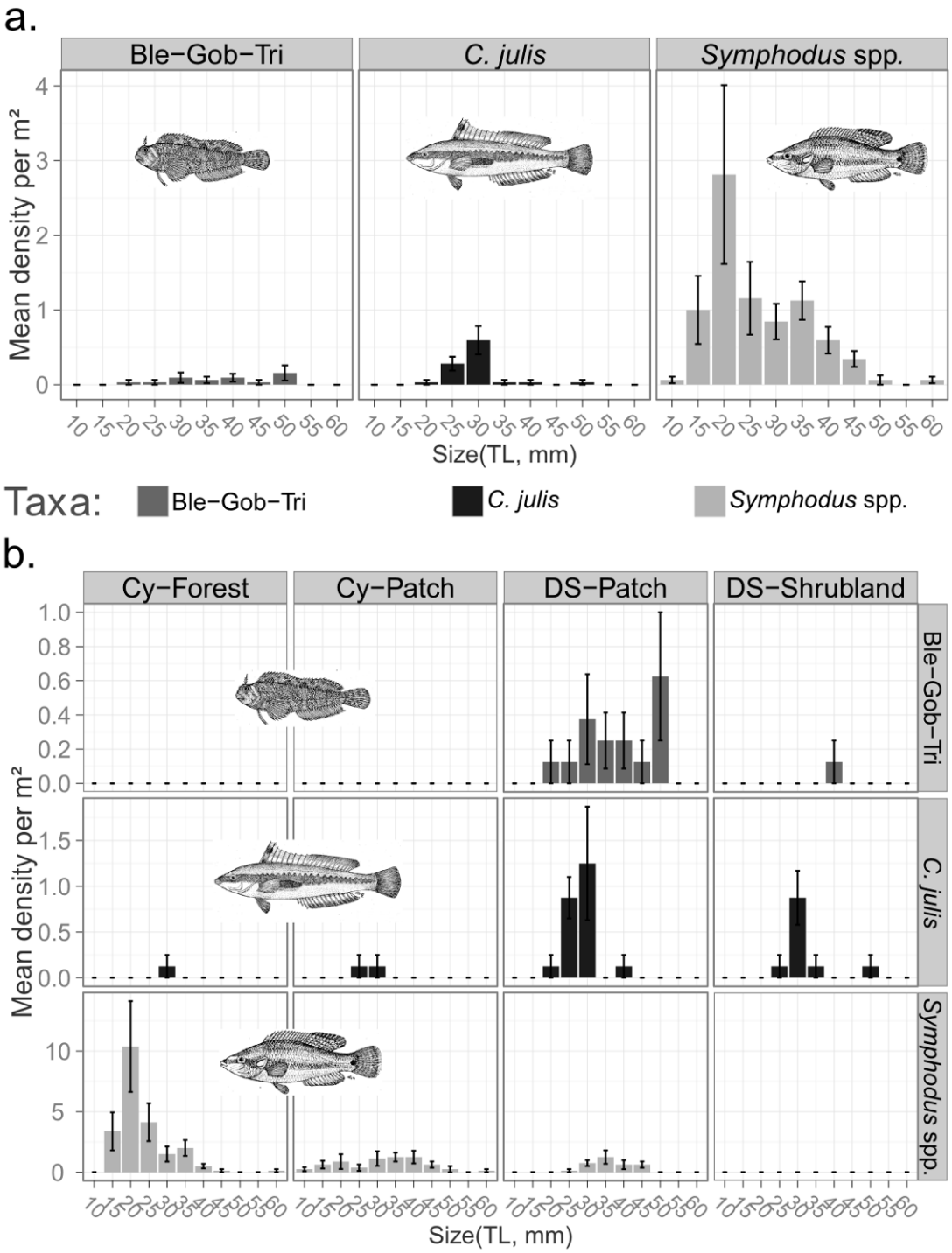


Fig. 32 : Frequent juvenile taxa size distribution : in overall (a) and by habitats (b)

Effects of habitats on juvenile assemblage composition

When looking at the relative abundance of the three observed taxa in each habitats, a significant effect of habitat on this assemblage composition could be detected: interaction term between habitat and taxa was significant (PERANOVA, $F = 14.43$, $P < 0.001$, Fig. 33 and pairwise tests results therein); in *Cystoseira* forest and patches, *Symphodus* spp juveniles were more abundant than other taxa, although these differences were less important in the

patchy *Cystoseira* habitat; within DS patches *Symphodus* spp. juveniles density was lower and the three taxa densities did not differ, while in DS wide bushland mainly *C. julis* juveniles were observed.

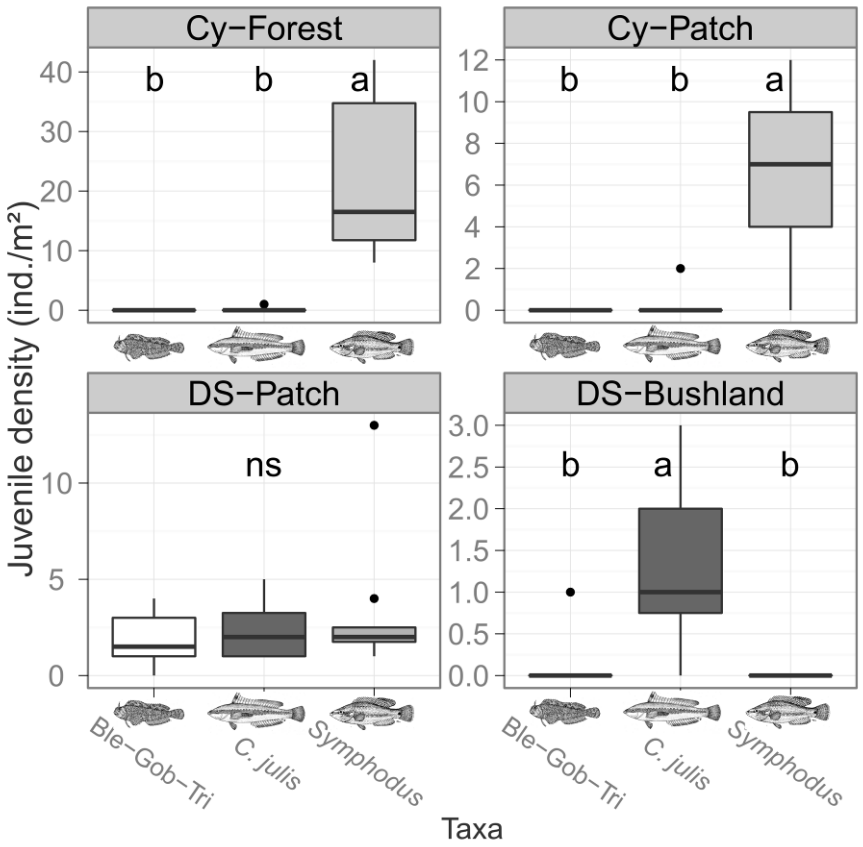


Fig. 33. Tuckey boxplot of juvenile densities per habitat and per taxa - pairwise tests results are shown (for a given habitat different lower case characters indicate significant differences between taxa).

Taxa-specific effect of habitats

As mentioned above, juvenile-density response to habitat was different according to taxa.
For *Symphodus* spp. juvenile densities were significantly higher in *Cystoseira* forest (22.1 ± 5.0 (se) ind./m²) than in patchy *Cystoseira* (6.8 ± 1.5 (se) ind./m²) or patchy DS (3.4 ± 1.4 (se) ind./m²), where densities were significantly higher than in wide DS bushland (no juveniles) (Fig. 34 and pair-wise tests therein). Interaction term between taxa, habitat and size-classes was significant (PERANOVA, $F = 6.32$, $P < 0.001$); for "small" *Symphodus* spp., the above pattern was observed even more strongly: densities decreased from forest to patchy-forest and from patchy-forest to patchy-DS (Fig. 35a and pairwise tests results therein). For "medium" *Symphodus* spp. this pattern was smothered, i.e. the three first habitat displayed low but equivalent densities of juveniles, significantly higher than in bushland (Fig. 35a). For the few "large" *Symphodus* juveniles observed, densities did not differ significantly between habitats. In other words, when looking at the other interaction of the same data (Fig. 35b) we observed for *Symphodus* spp. juveniles that patterns of

relative abundance of size-classes are opposed in the forest *vs.* in the DS-patches: in the forest small individuals are dominant *vs.* medium individuals, equivalent in the *Cystoseira* patches while in DS patches medium juveniles are more abundant than small ones (Fig. 35b and pairwise tests results therein).

For *Coris julis*, total juvenile densities in the patchy DS (2.4 ± 0.5 (se) ind./m²) were almost significantly higher than in the DS bushland (1.3 ± 0.4 (se) ind./m²) (pairwise test, p = 0.106), and both these habitats displayed significantly higher densities than *Cystoseira* forest or patches (Fig. 34 and pairwise-test results therein). *C. julis* "small-medium" juveniles displayed a density pattern among habitats equivalent as for total juveniles, while no significant differences appeared for "large" individuals (Fig. 35).

Blennioidei and Gobioidei juveniles were observed in significantly higher densities in the DS patches (1.9 ± 0.5 (se) ind./m²) than in the DS bushland while no individuals were observed in both *Cystoseira* habitats (Fig. 34), and it is worth noting that in the DS bushland only "large" (i.e. >40 mm TL) (although few) individuals were observed (Fig. 35b).

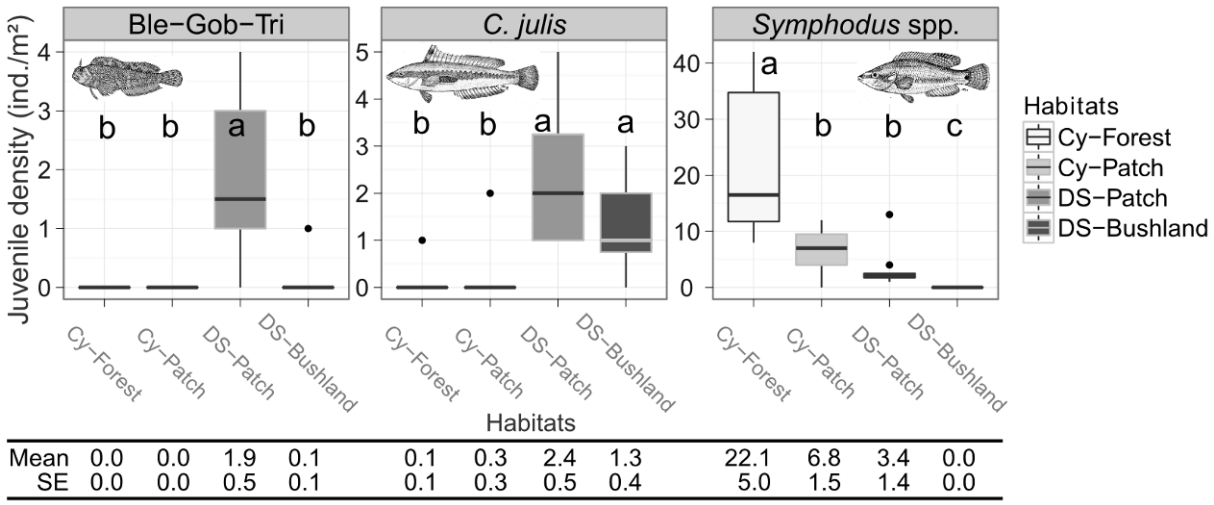


Fig. 34. Tuckey boxplot of juvenile densities per taxa and per habitat - pairwise tests results are shown (for a given taxa different lower case characters indicate significant differences between habitat) – for each habitat mean (se) of taxa specific juvenile density are given.

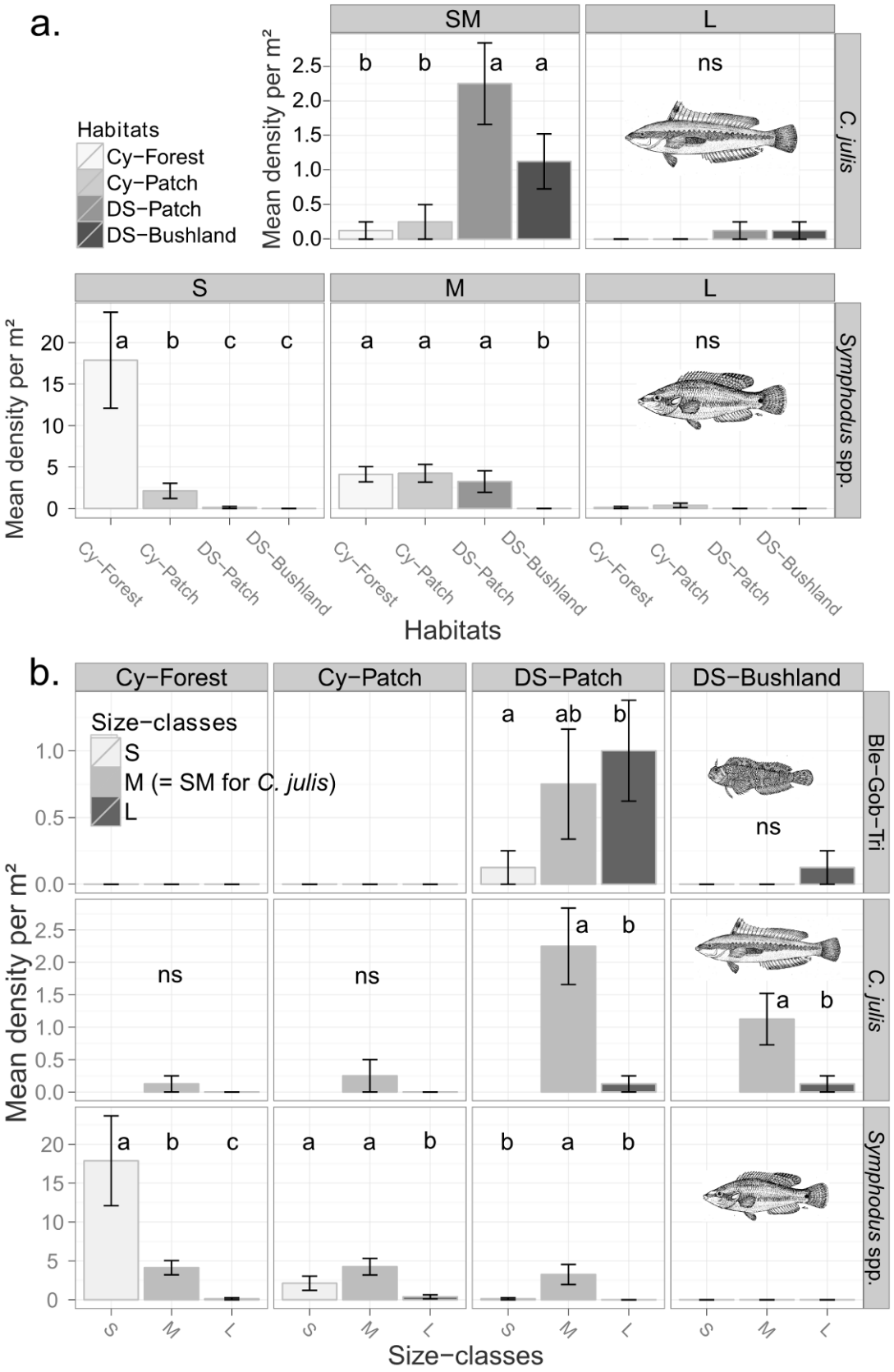


Fig. 35 : Mean (se) juvenile densities per taxa, per size-classes and per habitat - pairwise tests results are shown - for a given taxa, for a given habitat (a) or a given size-class (b) density bars sharing at least one lower case character are not significantly different – size-classes: SM = small-medium, S = small, M = medium, L = large (see definitions in M&M).

DISCUSSION

Both our experimental data and observations in natural habitats demonstrated that *Cystoseira* forests alteration negatively affected the juvenile fish assemblage composition qualitatively and quantitatively: any decrease in patch-density and patch-size in artificial habitats led to a decrease of several juvenile species densities, including the most abundant taxa in overall habitats (*Symphodus* spp.) and other species of commercial interest (*Serranus* spp.). Few taxa (and those displaying low overall abundances) showed increased densities in the altered habitats (e.g. *Mullus surmuletus*). These impacts of habitat transformations on juvenile assemblage was visible also as it lowered species richness: in both experiments richness increased through time, reflecting the settlement of species in the study area through seasons, but smallest patch-size treatments showed lowered richness. We could not conclude on any effect of patch-density on richness. Similarly, total density of all taxa pooled together was negatively impacted by both patch-density and patch-size reduction. Richness, total abundances of all taxa, assemblage composition and taxa specific densities showed no differences between treatments during the first months, when juveniles are not all present, but subsequently, as juveniles settle (detected notably by an increase in total abundance), forest depletion effect appeared clearly: juveniles colonized in majority the denser and larger patches.

For *Symphodus* spp. (i.e. *S. roissali, S. tinca* and *S. ocellatus*) forest fragmentation in natural habitats was associated to reduced juvenile densities; this was confirmed experimentally by similar results in case of patch-density and size reduction in artificial habitats. Notably, sparse patches (32 artificial *Cystoseira*/m²) displayed lower juvenile densities than Dense patches (160 artificial *Cystoseira*/m²). During the pilot experimental study with artificial *Cystoseira* (in 2009[6]) no differences appeared between the "Dense" (100% cover) and the 2009 prototype of "sparse" treatment displaying 48 artificial *Cystoseira*/m² (i.e. about 60% cover). In another study using artificial macrophytes, Worthington et al. (1991) found that reduction of leaf density had an effect on fish juvenile densities only under a given threshold level. We may similarly deduced, at least for *Symphodus* spp., that the threshold density at which artificial *Cystoseira* forest may start to lose its function for juvenile is situated between 48 and 32 *Cystoseira*/m², i.e. between 60% and 30% cover. We may not directly infer quantitative conclusion from this for natural forests, but at least it appeared that as soon as the continuous cover of the canopy is transformed into a truly sparse cover, its nursery value may decline. This was confirmed by others observations in natural *Cystoseira* forests, where *Symphodus* juvenile densities were positively correlated to *Cystoseira* forest

[6] See chapter III-part 2

percent cover and canopy height (unpublished data[7]). Considering patch-size, natural wide *Cystoseira* forests (i.e. >16 m²) hosted three times more juveniles than patchy forests (~4 m²): 22.1 ± 5 *vs* 6.8 ± 1.5 mean (se) juveniles per m². Given our experimental data, patch-size reduction for smaller patches (<1m²) also caused decreasing densities of juveniles. As a conclusion, although a threshold level of forest patch-size may not be inferred from our data, it appeared that any fragmentation of the initially wide natural *Cystoseira* forests reduces its nursery value –*sensu* Beck et al. (2001)- for *Symphodus* spp.

Moreover, for *Symphodus* spp., when looking for example at panel of boxplots of juvenile density per treatments, it appeared notably that significant differences between treatments were observed more particularly at settlement peak, i.e. notably when "small" juveniles are the most abundant (June-July and August-September): young settlers preferably settled into the denser and larger forests. Similarly, both patch-size and patch-density treatments had even stronger effect when looking only at small size-class juveniles. In natural habitats as well, negative effects of fragmentation upon juvenile densities were stronger for the small size-class of juveniles; while small juveniles were more abundant in the forest than medium and large ones, this trend reversed in the patchy forest and only medium juveniles were present in the DS patches. In summary, smallest, early settled *Symphodus* juveniles seemed to rely more particularly on the denser and wider forest. Furthermore, individuals had mostly "temporary" behavior rather than "permanent" on sparser and smaller patches, even more particularly if they were "small" juveniles. Our interpretation of these patterns claims that smallest juveniles seek more particularly shelter against predation, and they find it in the densest and widest forest, which tri-dimensional structure offers better refuges than sparse and small patches of forest. This interpretation is confirmed by our observations in 2009 of small juveniles that were less abundant in the sparse *Cystoseira balearica* forest than in the dense *C. crinita* forest (Cheminée et al., under review)[8]. If such refuges are not available (for example in sparse forest) juveniles may be less safe and consequently become more mobile, adopting a "temporary" behavior as we observed in artificial habitats, switching from one place to the other. This behavior has also been observed in natural Dictyotales - Sphacelariales bushland habitat in other Corsican sites (first author unpublished data).

Differential mortality and active habitat choice by juveniles are both induced by differences in habitat quality in terms of food accessibility and predation rate (Hindell et al., 2000). The best habitat minimizes juvenile mortality rate by optimizing the ratio between food accessibility and predation rate (Dahlgren and Eggleston, 2000). In our study case, habitats transformation is consequently detrimental to *Symphodus* recruitment and population replenishment since it probably lowered this ratio: on one hand depletion of *Cystoseira*

[7] See Chapter III part 3

[8] See chapter III part 2

forest may increase predation rate (Thiriet et al., accepted)[9] since it is lowering refuge available, making juvenile more vulnerable to predators, and on the other hand it also decreases food accessibility by making juveniles more mobile (temporary behavior observed here), i.e. allowing less time for foraging.

For *Coris julis* and also for *Symphodus cinereus*, all size-classes pooled, patch-size and density treatments did not have a clear effect on taxa-specific juvenile densities. Mainly a temporal trend was detected corresponding to the gradual arrival of settlers. However, *S. cinereus* juveniles tended to display more affinities to bare substrate rather than to any of the forested treatments: densities of juvenile were the highest on the short DS turf covering the bare substratum and moreover juveniles were mainly "temporary" on each of the forested treatments while they became "deambulatory" on bare substratum. This behavior is consistent with adults' behavior that are known to forage and even nest on unvegetated sandy substratum (Lejeune, 1985). For *Coris julis*, if looking at density per size-classes, it appeared that early settlers (smallest observed juveniles) were present only on the denser treatments, and subsequently that small-medium juveniles displayed more affinities for intermediate levels of forest densities during the first month following settlement (August) before to switch towards Bare plots when becoming larger (L size-class). This affinity of young *Coris* juveniles for the forest was confirmed by our observations in the natural environment: in Garganellu islet (Corsica) we observed that crypto-benthic species (Ble.-Gob.-Tri.) and *Coris* juveniles, for the smallest size-classes, were more abundant in the DS patches adjacent to patches of *Cystoseira* than in the wide and homogenous DS bushland. This was true although DS cover and height was lower in the patches than in the wide bushland. We conclude that higher juvenile densities in the DS patches was due to edge effect: the adjacent *Cystoseira* forest patches may offer them refuges in case of a pursuit predator detection (Horinouchi et al., 2009b) while the DS patches provides foraging ground (Guidetti, 2004). For crypto-benthic species, juveniles were observed almost only in the DS patches. Only large juveniles were seen in the wide DS bushland and none in the *Cystoseira* forest or patches. We hypothesize that *Cystoseira* under-canopy space may host high densities of these taxa juveniles, not detected in our counts since the method is not the best fitted for crypto-benthic species; juveniles may go out in the DS patches to forage, but may not dare to dwell into the wide DS bushland far from the protection of the *Cystoseira* canopy under which to retreat in case of predator detection. We conclude that *Coris julis* and crypto-benthic juveniles, at settlement, also require the refuge provided by the *Cystoseira* forest although they may as well forage in adjacent open patches of DS. This is consistent with previous observations (first author unpublished data), where *C. julis* juveniles densities in a *Cystoseira* dominated assemblage were correlated with increasing Dictyotales-

[9] See Chapter III part 5

Sphacelariales percent cover[10]. Crypto-benthic species densities in the forest should be studied more deeply using better fitted methods, current research lead e.g. in the frame of P. Thiriet PhD thesis explores this issue[11].

Serranus spp. juveniles also relied on the forest but probably for other reasons: juveniles were observed only on Dense or sparse patches in 2010, and on largest patches in 2011. When observed, it was mostly on the edge of the forest patches. In natural habitats, *Serranus* juveniles were as well observed on the edge of forested habitat (unpublished data[12]). We interpret this behavior as the manifestation of their stalk-attack predation tactic. *Scorpaena porcus* and *Muraena helena* young individuals, although not observed in high densities, when present, where systematically observed in the densest and largest patches of forest. We hypothesize that juvenile *Serranus* spp., *S. porcus* and *M. helena* rely as well on the *Cystoseira* forest, as a foraging habitat where they can find their prey with various predation tactics (Horinouchi et al., 2009b; Schultz et al., 2009); for example *Serranus* spp., as a stalk-attack predator, is patrolling at the edge of the forest, performing sudden and medium range attack-runs on any prey heading out the forest cover (pers. obs.).

As demonstrated for *Symphodus* spp. in our other *ex-situ* study (Thiriet et al., in prep.[13]), juvenile abundance pattern across habitats (i.e. *Cystoseira versus* DS) are explained partly by active habitat choice and by differential predation success on them. In the Mediterranean, if *Cystoseira* forests totally disappear in the future, juveniles will cope with the other habitats left, i.e. for rocky bottoms mainly DS assemblages. Along the continental coast of France for example, i.e. Marseilles or Albères rocky shores, *Cystoseira* forests have mainly disappeared (Thibaut et al., 2005), but Labridae or Serranidae juveniles and adults are still observed frequently in the rocky Infralittoral of these localities; for example Letourneur et al. (2003) described in Marseilles shallow (0-10 meters) rocky bottoms the positive correlation between juvenile labrid densities with the cover of "macroalgae" (i.e. DS), rubble and small blocks. This implies that fishes may survive in infralittoral habitats exempt of *Cystoseira*, however, the overall quality –*sensu* Hindel *et al.* (2000)- of the remaining habitats (i.e. DS) is probably lower: for *Symphodus* spp. not only predation success on them is higher due to less refuges offered by the DS tri-dimensional structure, but as explained previously their food accessibility may be lowered as well; such lower habitat quality (i.e. the lowered ratio food availability/predation rate) probably causes infralittoral rocky habitats to be less fitted for biomass production of these low trophic level fish species. Simultaneously, higher trophic

[10] See chapter III part 3

[11] See perspectives in chapter VI

[12] See Chapter III part 4

[13] See chapter III part 5

level species, such as the predatory *Serranus*, *S.porcus, M. helena* may also be affected by the lowered biomass of their prey taxa living usually in the disappeared forests.

As a conclusion, a dramatic loss of biomass production has probably already happened in areas where *Cystoseira* forests have disappeared, with consequences for the whole ecosystem and commercial fisheries. The exact quantification of how much productivity is virtually lost because of the absence of the forests is a priority task for future researches.

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4.3 Does loss of habitat heterogeneity and complexity alter fish recruitment? Preliminary results from the Mediterranean example of Caulerpa taxifolia invasion

In prep. for submission to Biological Invasions

Note :

For this paper, field surveys were performed during the Master thesis of Patricia Meyer (2001). Data analysis, interpretation and discussion were performed during my PhD thesis. This paper is part of projects FOREFISH and CIRCE, respectively founded by Total Foundation and the Agence de l'Eau Rhône-Méditerranée-Corse.

Does loss of habitat heterogeneity and complexity alter fish recruitment? Preliminary results from the Mediterranean example of *Caulerpa taxifolia* invasion

In prep.

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ABSTRACT:

Human activities may induce the presence and spread of marine invasive species that can transform and homogenize habitats. This in turn can alter fish recruitment and the subsequent replenishment of adult assemblages. We experimentally quantified the impacts of loss of habitat complexity on fish recruitment due to the invasion by the habitat-forming macroalga *Caulerpa taxifolia* (Chlorophyta) over fish (Teleostei) recruitment. Of the fourteen species of fishes were observed during the experiment, only two species of labrids (*Coris julis* and *Symphodus ocellatus*) settled in abundance. The temporal trend of juvenile densities suggested highest mortalities of *C. julis* juveniles in the least complex treatments. These results imply that loss of habitat complexity induced by invasion of *Caulerpa taxifolia* reduces fish recruitment and might reduce subsequent adult assemblages' replenishment.

KEY WORDS: *Caulerpa invasion,* habitat transformation, complexity, fish recruitment, mortality, *Coris*, *Symphodus*,

INTRODUCTION

Habitat complexity (i.e. the three-dimensional arrangement of structures that form habitat) is an important influence on species diversity and abundance (Harborne et al., 2011a) and behavior (Harborne et al., 2011b) . Typically, habitats with greater complexity can support more species and more individuals (see e.g. Atrill et al. (2000) or Horinouchi and Sano (1999)). Many species have very specific microhabitat requirements, which vary among species and life history stages (i.e. ontogenetic shift in habitat use) (Vigliola and Harmelin-Vivien, 2001). In the Mediterranean it was demonstrated that juvenile fishes of some species of the family Sparidae (*Diplodus* spp.) share in space and time shallow nursery microhabitats since *D. puntazzo*, *D. vulgaris* and *D. sargus* succeed in time in the same shallow gently sloping nursery habitat which substratum is made of heterogeneous blocks, boulders and pebbles, while D. *annularis* settle in the adjacent seagrass meadows (Garcia-Rubies and Macpherson, 1995; Guidetti, 2000; Harmelin-Vivien et al., 1995; Macpherson and Zika, 1999).

Consequently, altering habitat complexity can have cascading effects on species composition and abundance[14]. Many shallow subtidal habitats in the Mediterranean Sea have been modified by anthropogenic impacts (Coll et al., 2010; Francour et al., 1999; Mangialajo et al., 2008; Milazzo et al., 2004b; Montefalcone et al., 2010; Rovere et al., 2009; Sala et al., 1998). These modifications include alteration of habitat complexity, by changing the composition of biotic and abiotic structural components. One example of such changes is the introduction of invasive habitat-forming species, such as *Caulerpa taxifolia* (Vahl) C. Agardh and *C. racemosa* var. *cylindracea* (Forsskål) J. Agardh, two species of benthic macroalgae (Chlorobionta) that have been introduced into the Mediterranean (Box et al., 2010; Francour et al., 2009; Klein and Verlaque, 2008; Levi and Francour, 2004; Longepierre et al., 2005; Molenaar et al., 2009). These species have invaded all coastal habitats (shallow or coralligenous (Cebrian et al., 2012) rocky reefs, sandy bottoms, seagrass meadows) which tend to be replaced and homogenized by *Caulerpa* spp. meadows and this has had an impact on fish assemblages: for example, while the species composition of fish assemblages has remained unchanged, their species richness, overall biomass and density have decreased substantially (Francour et al., 1995). This has been attributed to a reduction in three-dimensional habitat complexity (Harmelin-Vivien et al., 2001). It has been suggested that the simple structure (low complexity) of *Caulerpa* spp. meadows, combined with the high density at which fronds grow within meadows reduces the complexity of habitats relative to natural rocky reef habitats (Harmelin-Vivien et al., 2001). This habitat simplification should be detrimental to fish assemblage because of the associated loss of shelter and food (Levi and Francour, 2004).

It is more particularly important to understand the consequences of these habitat modifications on settlement and recruitment processes since they are key steps in fish life

[14] see chapter IV-part 2

cycle and therefore determine fish stocks replenishment. In our study, settlement is defined as the arrival of early juvenile (post-larval) fishes (referred as “settlers”) within benthic habitats after their pelagic larval phase. Recruitment corresponds to the subsequent incorporation of these juvenile fish into adult populations after their survival in nurseries and migration towards adult habitats (referred as “recruits”) (Beck et al., 2001; Levin, 1994; MacPherson, 1998). We use the term “juvenile” to encompass individuals present in the nursery habitats after settlement and until their dispersal (Cheminée et al., 2011). The maximum density of settlers is the best index for the intensity of settlement events, i.e. the number of new individuals joining the benthic habitat in a given area. However it does not necessarily reflect the final abundance of juveniles that recruit into the adult population, because the initial number of settlers might be highly depleted through mortality (Macpherson et al., 1997). Macpherson (1998) defined recruitment level as the number of juveniles remaining at the end of the post-settlement period. However this does not take into account mortality of juveniles during their transition from nurseries toward adult habitats (Beck et al., 2001). A proxy of recruitment success is the number of juveniles surviving arbitrary periods of time after settlement (Levin, 1994a; Levin, 1994b; MacPherson, 1998); this can be assessed by monitoring abundance of juveniles over the post-settlement period in the nursery until their dispersal towards adult habitats (Macpherson et al., 1997).

In this paper we aim to quantify of the effect of differences in habitat complexity, including that of the invasive alga *Caulerpa taxifolia*, on fish settlement and recruitment. If the primary mechanism for the negative effect of *Caulerpa* is habitat simplification (i.e. reduced complexity), then one simple prediction is that any increase in complexity in a *Caulerpa* meadow should result in an increase in densities and survival of juveniles (Connell and Jones, 1991): this was the hypothesis that we tested. We used a manipulative experiment in order to artificially increase habitat complexity in a *Caulerpa* meadow, using arrangements of concrete blocks. In order to test our hypothesis we studied temporal trends of densities of fish juveniles in these manipulated habitats of different complexities.

MATERIAL AND METHODS

Study site, treatments and experimental design

The study was carried out along the coast of Cap Martin near Menton, France (north-western Mediterranean; 7°30'E; 43°45'N). The study site was composed of flat, gently-sloping sandy bottoms, covered by a dense *Caulerpa taxifolia* meadow, at 10 meter depth. After its first appearance in the Mediterranean in 1984 in Monaco (Meinesz and Hesse, 1991), *C. taxifolia* invaded the study site in the 90's (Francour et al., 1995; Meinesz et al., 1998) and formed large homogenous meadows (more than 90% cover) from 5 to 15 m depth.

We used concrete blocks (20x20x50 cm) to manipulate habitat complexity within the *Caulerpa* meadow. Blocks were arranged on the bottom, in the *Caulerpa* meadow, and we manipulated the density of blocks, to create treatments of four complexities (Table 1). Each treatment was built by randomly spreading the blocks over a 2x20 m area parallel to the coast. Treatments were arranged in two parallel lines separated by 10 meters; each line contained one replicate for each treatment, and each replicate was separated by 3 meters. In one line the treatments were arranged from the highest to the lowest complexity; in the other line, the order was reversed. Overgrowing *Caulerpa taxifolia* fronds were regularly hand removed by Scuba divers.

Table 1. Habitat complexity treatments used in the manipulative experiment (replicates n = 2)

Treatment	Number of blocks
High complexity (H)	21
Medium complexity (M)	14
Low complexity (L)	6
Very low complexity (V)	0

Fish counts

Fish counts were performed weekly from August 2000 to February 2001 (N = 18) when weather and diving conditions permitted. Counts were done by means of underwater visual census (UVC), by SCUBA divers at 0.5 m above the substrate; each replicate was censused in <5 minutes. All counts were made when visibility exceeded 3 m, and between 9 am and 11 am, a timeframe within which studied species were active and easily observed (i.e. not hiding between *C. taxifolia* fronds). Fish abundance was counted up to 10 individuals. Above 10 individuals, density estimate groups such as 10-20, 20-50, 50-75 and 75-100 individuals were used (Francour, 1999).

Ten to 14 fish species belonging to the families Labridae, Serranidae and Sparidae were recorded (Table 2). The Labridae *Coris julis* and *Symphodus ocellatus* were the only two species to settle and recruit during the experiment and so we consider only these two species in this study. We categorized individuals into three size classes (small, medium and large fishes; each class encompasses 1/3 of the total maximum length), and further subdivided the "small" size class into "settlers", "post-settlers" and "recruits".

Table 2. Fish assemblages composition and frequency of occurrence of the different species recorded on each habitat treatments between August 2000 and February 2001 (n = 18)

Family	**Species**	**Treatments**			
		H	**M**	**L**	**V**
Labridae	*Coris julis*	1.00	1.00	0.89	0.92
	Symphodus ocellatus	0.97	0.94	0.83	0.83
	Symphodus tinca	0.58	0.36	0.33	0.19
	Symphodus roissali	0.03	0.06	0.03	0.08
	Symphodus melanocercus	-	-	0.03	-
	Symphodus rostratus	0.17	0.08	0.06	0.03
	Symphodus cinereus	0.14	0.11	0.03	0.06
	Labrus spp.	0.28	0.14	0.19	0.19
Serranidae	*Serranus cabrilla*	0.61	0.58	0.53	0.39
	Serranus scriba	0.36	0.28	0.33	0.25
Sparidae	*Diplodus annularis*	0.14	0.19	0.19	0.22
	Diplodus vulgaris	0.08	0.14	0.03	-
	Diplodus puntazzo	-	-	0.03	-
	S. cantharus	-	-	0.06	-
No. Species		**11**	**11**	**14**	**10**

Data analysis

Variation of densities of each species among treatments (habitat complexity : H>M>L>V; see Table 1) and through time, for the period running from the time of peak abundance of a given size-class until dispersal of those same individuals, can be used in order to infer differences in mortality rates between treatments (Macpherson et al., 1997). To standardize for differences of fish abundance between treatments (n=2 for a complexity level), we expressed abundances as the percentage of the maximum abundance per treatment.

Because assumptions of normality and homogeneity of variances were not fulfilled to allow the use of parametric statistical test, the Scheirer-Ray-Hare test, a non-parametric alternative to two-way ANOVA (Sokal and Rohlf 1995), was used to compare relative abundances between the four treatments and between temporal censuses of the period running from the time of peak abundance. This test was followed by a non-parametric post-hoc test for pairwise comparisons (Siegel & Castellan, 1988, p213) in order to determine the nature of differences among treatments and temporal censuses. Separate analyses were conducted for each size classes of each species. All statistical analyses were performed using the R 2.12.2 statistical software (R Development Core Team, 2011).

RESULTS

For both *Symphodus ocellatus* and *Coris julis*, the size classes settlers, post-settlers and recruits succeeded each other sequentially from the start of the sampling period (Fig. 1). In all treatments, the peak of *C. julis* abundance was recorded on the 27th September (day 56) for settlers, the 3th October (day 62) for post-settlers and 24th October (day 83) for recruits; For *S. ocellatus*, these maxima were recorded on the 19th September, 3th October and 24th October respectively (days 48, 62, 83). Individuals belonging to medium and large size classes were recorded during the entire survey period (August to February) and their mean densities did not show significant differences between treatments or dates (Scheirer-Ray-Hare test; both $p > 0.05$). The maximum densities recorded for medium and large size classes were 1.62 and 0.37 ind./10 m² for *C. julis* and 3.50 and 0.50 ind./10 m² for *S. ocellatus*.

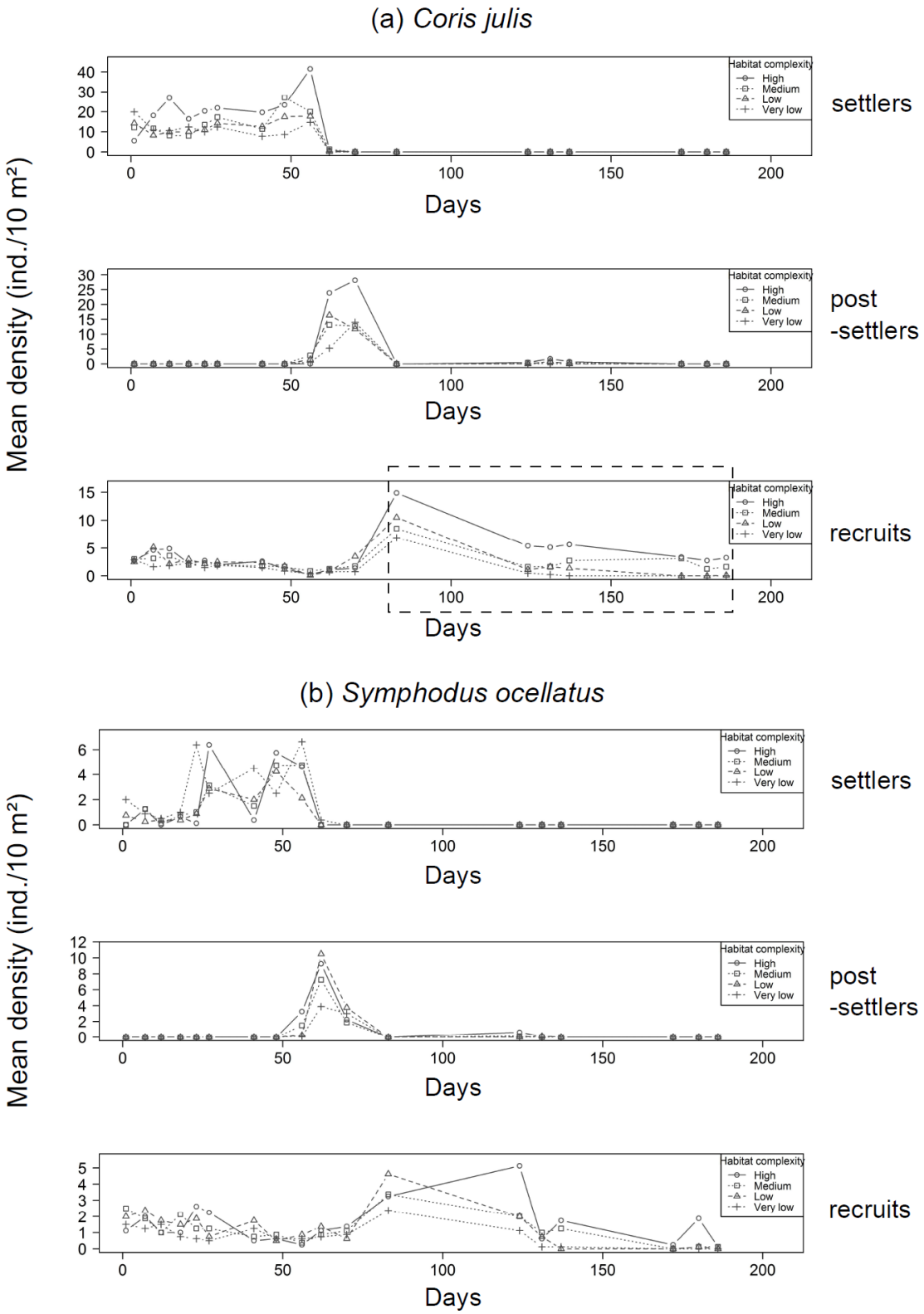

Fig. 1. Mean density (n=2) at different survey dates of (a) *Coris julis* and (b) *Symphodus ocellatus* settlers, post-settlers and recruits in each habitat complexity treatment. Dashed-line rectangle: see detailed view and error bars (S.E.) for *C. julis* recruits on Fig. 2.

Following the peak abundance for each size class of each species, significant differences in relative abundance between treatments were apparent only for the recruits size class of *Coris julis* (Scheirer-Ray-Hare test, H=11.06, Df=3, p = 0.011, Table 3); densities of other size classes for this species and all size classes of *Symphodus ocellatus* only differed according to temporal census (Table 3). Pairwise comparisons of recruits *C. julis* densities revealed that densities in habitats H and M (the most complex) were significantly higher than in habitats L and V (the least complex) (post hoc test, $p < 0.0001$, Fig. 2); they did not differ significantly between habitats H and M, and between habitats L and V respectively (post hoc test, $p > 0.05$).

Table 3. Scheirer-Ray-Hare tests analysing effects of habitat complexity treatments and temporal censuses on densities of *Coris julis* and *Symphodus ocellatus* for the settlers, post-settler and recruits size classes. Significant effect ($p < 0.05$) are marked by an asterisk. Df refers to degrees of freedom

Species	Size class	Explanatory variables	Df	Sum Sq.	Mean Sq	*H*	*p* value
Coris Julis	Juvenile	Habitat complexity	1	6.90	6.91	0.04	0.838
		Temporal censuses	10	3403.50	340.35	20.63	0.024*
		Residuals	32	410.10	12.82	2.49	1.000
	Very small	Habitat complexity	3	89.33	29.78	0.80	0.848
		Temporal censuses	8	2825.37	353.17	25.45	0.001*
		Residuals	24	299.79	12.49	2.70	1.000
	Small	Habitat complexity	3	748.29	249.43	11.06	0.011*
		Temporal censuses	6	800.50	133.42	11.83	0.066
		Residuals	18	243.21	13.51	3.59	0.999
Symphodus ocellatus	Juvenile	Habitat complexity	3	37.90	12.64	0.23	0.973
		Temporal censuses	10	3242.00	324.20	19.65	0.033*
		Residuals	30	235.10	7.84	1.42	1.000
	Very small	Habitat complexity	3	37.72	12.57	0.34	0.952
		Temporal censuses	8	2330.00	291.25	20.99	0.007*
		Residuals	24	362.28	15.10	3.26	1.000
	Small	Habitat complexity	3	309.43	103.14	4.57	0.206
		Temporal censuses	6	1269.25	211.54	18.76	0.005*
		Residuals	18	214.32	11.91	3.17	1.000

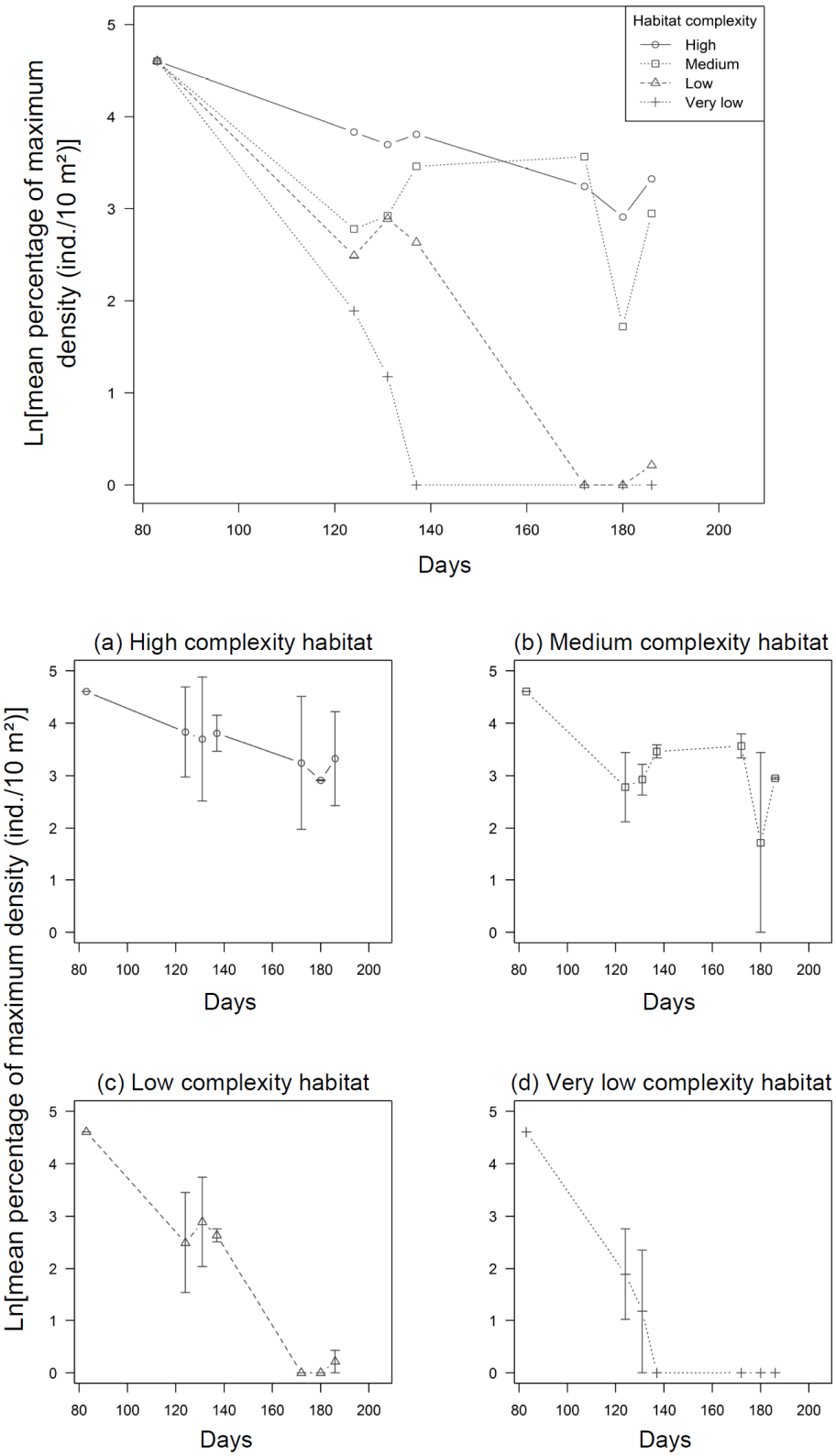

Figure 2: Relative abundance of *Coris julis* recruits from the date of peak abundance (day 83) for each habitat. The Y-axis is expressed as the Ln-transformed mean proportion of the initial density at the peak – (a) to (d): detailed representations with error bars = SE (n = 2).

DISCUSSION

Mediterranean fish assemblages rely on the complementarities and the synergies of a complex mosaic of habitats and microhabitats suitable as nurseries for juveniles of different species (Cheminée et al., under review; Thiriet et al., accepted). In invaded sites, *Caulerpa taxifolia* tends to homogenize the seascape and reduce the diversity of habitats and microhabitats available (Harmelin-Vivien et al., 2001). In our study, only two species (*Coris julis* and *Symphodus ocellatus*) among the fourteen observed settled in *C. taxifolia* meadows in substantial abundance: seascapes dominated by *C. taxifolia* may be less suitable for juveniles of the other species and therefore have a lower nursery value – *sensus* Beck et al. (2001) – than uninvaded ones.

During our study, densities of *C. julis* were consistently higher than those of *S. ocellatus* in all treatments. In *Cystoseira* spp. forests the reverse has been observed (Cheminée et al., under review): juveniles of *S. ocellatus* were consistently more abundant than those of *C. julis*. We hypothesize that the larger body size of *S. ocellatus* impairs their ability to hide between *Caulerpa* thalli; this restriction might not apply to the thinner *C. julis* individuals. The inter-thalli void (spaces between and under thalli) may indeed be larger below a *Cystoseira* sp. canopy than a *C. taxifolia* canopy, although this has not been measured. If true, as seems likely, it may offer suitable refuges only for the small-bodied individuals such as *C. julis*.

The density decrease of *C. julis* and *S. ocellatus* individuals in all treatments was not accompanied by increased densities in surrounding areas (authors' unpublished data): we therefore believe that inferences about mortality rates, rather than migration, are robust. For *S. ocellatus* the absence of significant differences between treatments might be due to low initial densities of individuals. In contrast, we infer differential mortality among treatments for *Coris julis* recruits, due to higher survival in the more complex habitats (Connell and Jones, 1991). Lower mortality might be due to (1) lower predation rate possibly because of a higher number of refuges available (Juanes, 2007; Piko and Szedlmayer, 2007) or (2) better nutrition due to greater amount of food items. In our experiment, treatments differed by the number of refuges available (related to the number of concrete blocks) but probably did not differ in food availability because blocks were regularly cleaned of any epibiota. We therefore hypothesize that the higher mortality we observed in the less complex habitats is due to higher predation in less complex habitat. However, the absence of significant differences between treatments for the smallest (settlers and post-settlers) size classes suggests that this did not equally affect fishes of all size classes, as previously shown for other species e.g. by Fisher et al. (2007). This might be because the smallest size classes (e.g. settlers) may still find sufficient shelter despite the loss of complexity, while bigger individuals (e.g. recruits) cannot. As for *Symphodus* spp., larger body-sized recruits of *C. julis* may not find sufficient space between thalli of *C. taxifolia* meadows; they may not be able to use it neither as a shelter habitat as opposed as in *Posidonia oceanica* meadows

(Garcia-Rubies and Macpherson, 1995) nor as a foraging habitat as opposed to Dictyotales and Sphacelariales shrubby assemblages (Cheminée et al., under review; Guidetti, 2004), and therefore may be more exposed to mortality by predation and/or starvation.

For the "recruits" size class of *C. julis*, mortality was highest in the two least complex habitats and no individuals remained during the last censuses, implying that mortality was 100%. This result is consistent with our initial hypothesis: loss of complexity, due to an invasive species, increases the mortality of juvenile fishes.

In conclusion, the loss of habitat complexity due to invasion of *C. taxifolia*, both at the scale of the seascape (=macrohabitat *sensus* Harmelin-Vivien et al. (2001)) and at the micro-habitat scale (inter-thalli void), may consequently be detrimental to the global nursery role of coastal areas because of increased mortality. High mortality of settlers and recruits might explain the lower densities of adults that have been observed in *C. taxifolia* meadows in comparison with uninvaded (and more complex) habitats (Francour et al., 1995; Harmelin-Vivien et al., 2001).

ACKNOWLEDGMENTS

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4.4 Chapter conclusions

For juveniles, the best habitat maximizes the ratio food accessibility/predation rate (Hindell et al., 2000). In our two case study (*Cystoseira* forest depletion and *Caulerpa* invasion) the resulting habitat transformations lowered this ratio: we highlighted this notably for *Symphodus* spp. in depleted *Cystoseira* forests (less refuge, less time to forage); and for *Coris julis* in *Caulerpa* meadows (less accessibility to substrate for foraging and less accessibility to inter-thalli void for sheltering). On the other hand, for *Symphodus* spp., fragmentation of *Cystoseira forests* was as well detrimental to recruitment. But in parallel habitat fragmentation increases the amount of ecotone and associated edge effects (Jelbart et al., 2006; Smith et al., 2011) which in our case was favorable for e.g. *Coris julis* or *Serranus* spp. juveniles. Such a juxtaposition of various micro-habitats is as well providing complementary habitats for various species, according to a spatial partition of habitat uses (Harmelin-Vivien et al., 1995). Consequently the best fish biomass production of infralittoral habitats, through recruitment, will rely on a subtitle equilibrium providing a compromise between these processes. Production may be maximum in environments (*sensus lato*) maximizing habitat tri-dimensional structure –*sensu* August (1983)- at both macrohabitat (i.e. seascape) scale (=heterogeneity) and micro-habitat scale (=complexity or tri-dimensional architecture)[15].

As a conclusion, understanding these processes and managing these habitats and their fish assemblages will require to work at nested spatial scales from the local to the global seascape picture. Chapter V addresses this issue.

[15] See discussion on heterogeneity and complexity in Chapter VI

Chapter V. Applications for coastal habitats management

Sormiou, Marseilles, 12th April 2004 – During summer it is common to observe more than 100 boats per day anchored in this cove ("Calanque"). Anchoring has been partly prohibited in the inner-most part in order to limit the impacts of frequentation on infralittoral habitats (e.g. *Posidonia oceanica* meadows, the dark patches on the picture). Recently in early 2012, the surrounding area was designated National Park.

Chapter V. Applications for coastal habitats management

5.1 Chapter introduction

Coastal management plans must notably protect essential habitats and their functions (nursery grounds, spawning grounds, etc.) in order to guarantee the replenishment of coastal fish assemblages. Once we know, for each species of interest, which habitats may play a nursery role (Chapter III), where and which amount of each nursery habitat is present along the coast (Chapter II), and what are the consequences of their transformations (Chapter IV), coastal managers may have the required information to adapt coastal development programs and design adequate protection plan. The present chapter addresses the questions raised in Chapter II: does the current spatial design of management measures take the spatial distribution of essential habitats for fishes and their connectivity into account? Although such a “seascape approach” has been long applied in tropical seas (Direction de l'Agriculture de Mayotte et al., 2002), it is more recent and even not yet implemented in the Mediterranean.

- The **first part (5.2)** of this chapter is a slightly modified and enriched version of an English written paper accepted for a Springer-Verlag Edition of the Proceedings of the Scientific seminar on “Seascapes” held in Brest "Séminaire scientifique et technique sur les paysages sous-marins" – Brest (France), 29 - 31 of March 2011. Although this article is not a proper discussion of the full thesis, its reasoning refers frequently to each of the previous chapters and it offers a synthesis of some of their outputs. More particularly it uses the example of *Diplodus* spp. nursery habitat.

- The **second part (5.3)** of this chapter is an extract of the “Atlas des zones de nourriceries de Sars (*Diplodus* spp.) et biocénoses marines du Parc National des Calanques” (in prep.). This atlas is based on data presented in part 5.2 and it compiles maps displaying both the spatial distribution of *Diplodus* spp. nursery habitats and infralittoral biocenosis. The maps provided correspond to various sites along the rocky shore of Marseilles (France). This part is the result of a collaboration I developed with the management team of the Calanques National Park. The aim of this atlas is to provide practical useful data on the spatial distribution of nursery habitats, which may allow managers to better target conservation efforts and feed further discussions for coastal management.

5.2 Gestion des habitats de l'Infralittoral : adopter une approche à l'échelle des paysages sous-marins

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Gestion des habitats de l'Infralittoral : adopter une approche à l'échelle des paysages sous-marins

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Introduction : la notion d'écologie du paysage et la gestion des espaces naturels littoraux

Le terme d'écologie du Paysage (Landscape Ecology) aurait été utilisé en premier par un géographe Allemand, Carl Troll (1939). Ce chercheur géographe, botaniste, physicien, géomorphologue s'est intéressé aux relations entre hétérogénéité des écosystèmes montagneux, la phytogéographie et les sociétés humaines. Ses travaux ont surtout été marqués par l'utilisation de la photographie aérienne pour analyser l'hétérogénéité des milieux physiques en lien avec les couvertures végétales des milieux montagneux. Si le terme a été utilisé relativement tôt dans l'histoire de l'écologie, ce n'est que dans les années 1980 que la discipline a vraiment émergé sous l'impulsion de la naissante IALE *(International Association for Landscape Ecology)*. Contrairement à l'écologie « classique » qui tentait de raisonner sur les populations et communautés évoluant dans des écosystèmes homogènes, l'écologie du paysage s'est construite autour de la prise en compte centrale de l'hétérogénéité spatiale et temporelle. Dans les années 80 les concepts théoriques de la discipline se sont essentiellement forgés sur l'analyse des paysages agricoles où les pratiques de l'agriculture influaient grandement sur la fragmentation des écosystèmes et le fonctionnement des populations.

Les concepts fondateurs de la discipline sont sans conteste issus de la théorie de la biogéographie des îles développée par McArthur & Wilson (1967), suivant laquelle des populations d'oiseaux étaient d'autant plus isolées et vulnérables que la taille de l'île était petite et isolée des autres îles. Ainsi, l'écologie du paysage s'est-elle intéressé dès le départ aux relations entre la fragmentation des habitats et la structure des populations ou des communautés. Cela a conduit Levins (1969) à développer l'un des concepts essentiels de l'écologie du paysage : celui de la « métapopulation ». Il stipule que dans des habitats fragmentés, les populations évoluant dans chacun des habitats sont plus ou moins isolées les unes des autres, en fonction de leur capacité à se disperser entre chacun des habitats séparés par d'autres habitats moins favorables à l'espèce. La taille des habitats définit la

taille des populations. Chacune des populations pouvant évoluer et se maintenir indépendamment des autres populations tant que son pool génétique est suffisamment grand. En dessous d'une certaine taille, la population périclite si elle n'est pas alimentée par les populations voisines. Les petits habitats accueillent donc souvent des « populations puits » dont la pérennité dépend des apports de gènes des populations voisines, plus grandes, qui se comportent alors comme des « populations sources ».

Ainsi, l'écologie du paysage s'évertue à comprendre les mécanismes, le plus souvent d'origine anthropique, qui conduisent à une structuration du paysage en agissant sur une fragmentation des habitats. Ces habitats étant organisés suivant une architecture en « matrice » (par exemple des champs cultivés) ou en « taches » (par exemple des bois). Ces écosystèmes forestiers relictuels peuvent être agencés de manière différente : suivant un continuum de forêts et bois interconnectés par un réseau bocager ou de manière discontinue.

La connectivité biologique entre les parcelles forestières dépend de la capacité de dispersion des organismes et de la structure du réseau paysager (formes, agencements …), de la nature des parcelles formant la matrice (par exemple taille des parcelles agricoles, type de culture) et de la distance entre les habitats forestiers. L'étude de la connectivité biologique est donc un volet fondamental indispensable à l'analyse en écologie du paysage : quelles sont les capacités des organismes à se disperser au travers des paysages ?

L'écologie du paysage s'est surtout intéressée, historiquement, aux écosystèmes terrestres afin de comprendre comment les biocénoses pouvaient se structurer dans le contexte des activités humaines liées notamment à l'agriculture et à l'urbanisme. Le transfert de la discipline aux écosystèmes marins est beaucoup plus récent, puisque le terme de « *Seascape* » n'est apparu que dans les années 1980 (Pittman et al. 2011). La principale difficulté réside dans la caractérisation des paysages sous marins limitée techniquement par un champ de vision restreint et les moyens d'observation disponibles.

Quand on considère une portion du littoral, les fonds marins de l'Infralittoral apparaissent sous la forme d'une mosaïque d'unités géomorphologiques et biologiques caractérisées par leurs composantes biotiques et abiotiques (Chapman, 1995) : en fonction de l'échelle et des composantes considérées on nomme ces unités écosystèmes, biocénoses, habitats, voire micro-habitats. Cette mosaïque d'unités compose un paysage, dont l'échelle peut être comprise entre une dizaine de mètres et une dizaine de kilomètres. Au sens des écologues un paysage sous-marin est donc une somme d'habitats dont les propriétés émergeantes sont différentes de la simple addition des propriétés de chaque habitat. En effet, l'une des propriétés émergeantes les plus significatives en écologie du paysage sous-marin est la connectivité entre ses unités qui dépend très fortement, comme en milieu terrestre, du niveau de fragmentation du paysage et des capacités d'échanges d'individus entre habitats

(Basterretxea et al., 2012b; Cowen et al., 2007; Di Franco et al., 2012; Gillanders et al., 2003; Mumby, 2006).

Cette notion pluridisciplinaire de paysages sous-marins est (ré-) apparue récemment notamment avec le récent essor d'une gestion publique des espaces marins (Musard O. comm. pers.). La nécessité d'une telle gestion répond à la multiplicité des acteurs, usages, pressions, et des menaces en résultant (surexploitation des ressources, destruction des habitats par sur-fréquentation ou remblaiements, pollutions, …). En zone littorale, véritable interface entre le milieu marin et la zone continentale, cet ensemble de menaces auxquels font face les paysages sous-marins (Coll et al., 2010) suscite des enjeux qui interpellent les scientifiques, les organismes gestionnaires et les décideurs publics.

Afin de mettre en œuvre la gestion d'un espace marin littoral donné, l'organisme gestionnaire qui en a la charge commence par analyser l'état initial de cet environnement, c'est à dire décrire les composantes naturelles de ce paysage, les usages humains qui en sont fait, les pressions et éventuellement les menaces résultantes pour ces composantes, tout en tenant compte des continuités avec le domaine terrestre. Ceci permet d'identifier des enjeux de gestion prioritaires, de proposer des objectifs de gestion et un plan d'action permettant, à travers la réalisation de mesures concrètes, d'atteindre ces objectifs. A l'heure de la démocratie participative, enjeux, objectifs et actions sont définis en concertation avec les différents acteurs du littoral (démarche Natura 2000 par exemple). Ce type de démarche visant le consensus contraste avec les politiques de « mise sous-cloche » qui primaient dans les années 70-80 (Francour et al., 2001).

Afin de définir des enjeux prioritaires, une des approches utilisées consiste à identifier au sein de la mosaïque paysagère les unités où les interactions entre composantes naturelles et pressions anthropiques engendrent des impacts (menaces) particulièrement préoccupants. Lors de cette analyse paysagère on cherche en particulier à savoir quelles sont les unités ayant une fonction « importante » (aussi bien du point de vue social, économique, qu'écologique) et qui subissent des pressions susceptibles de menacer cette fonction et ainsi d'engendrer un coût probable important (social, économique, ou écologique). A travers l'œil du scientifique écologue, les unités (vues comme des habitats) devant être considérées comme prioritaires sont entre autres celles qui ont une fonction écologique clef : dans le cas des poissons (Téléostéens) par exemple, ce sera les zones de frayère des adultes (Koenig et al., 2000) ou les zones de nourriceries des juvéniles (Beck et al., 2001; Cheminée et al., 2011; Harmelin-Vivien et al., 1995), car elles sont considérées comme indispensables au renouvellement des populations. Dans le but de gérer la ressource « poissons », le plan de gestion devra alors inclure une protection de ces habitats « clef », c.a.d. essentiels pour le cycle de vie des espèces. Cette nécessité de protéger les habitats pour protéger les espèces est de plus en plus comprise et intégrée dans les processus de gestion internationaux (e.g. la directive Habitats intervenant dans la démarche Natura 2000) ou nationaux (e.g. Arrêté du

29 octobre 2009 fixant la liste des oiseaux protégés sur l'ensemble du territoire et les modalités de leur protection, qui stipule dans son article 3 que les interdictions envisagées s'appliquent aux éléments physiques ou biologiques réputés nécessaires à la reproduction ou au repos de l'espèce considérée).

Cependant cette réflexion se fait au mieux à l'échelle d'un habitat, ou seulement à l'échelle des habitats essentiels à une seule espèce : la dynamique globale et les interactions entre unités de la mosaïque paysagère ne sont pour l'heure pas ou rarement prises en compte. Pourtant, c'est en réalité un chapelet d'habitats qui devraient être pris en considération lors de la définition des enjeux et actions de gestion afin de prendre en compte l'ensemble des habitats essentiels à chaque étape du cycle de vie, pour chacune des espèces d'intérêts. Au cours de leur cycle vital, les organismes vivants vont en effet occuper successivement les habitats écologiques essentiels à chacune des phases de leur existence (Fig. 1). Les habitats essentiels habituellement pris en considération sont les frayères (zone de reproduction), les nourriceries (zone de croissance des juvéniles), les zones d'alimentation (croissance des adultes), de repos (estival ou hivernal) et des habitats de dispersion qui deviennent des corridors lorsqu'ils sont confinés. Le passage entre ces habitats se fera suivant des mécanismes de dispersion qui peuvent être diffus ou concentrés dans des espaces confinés. Tout un continuum de stratégies existe allant d'espèces résidentes (Fig. 1 ; repère a), où toutes les phases du cycle de déroulent dans le même habitat, aux espèces migratrices (Fig. 1 ; repère b) dont les histoires de vie seront marquées par le passage d'un habitat à un autre afin d'y accomplir différentes étapes essentielles.

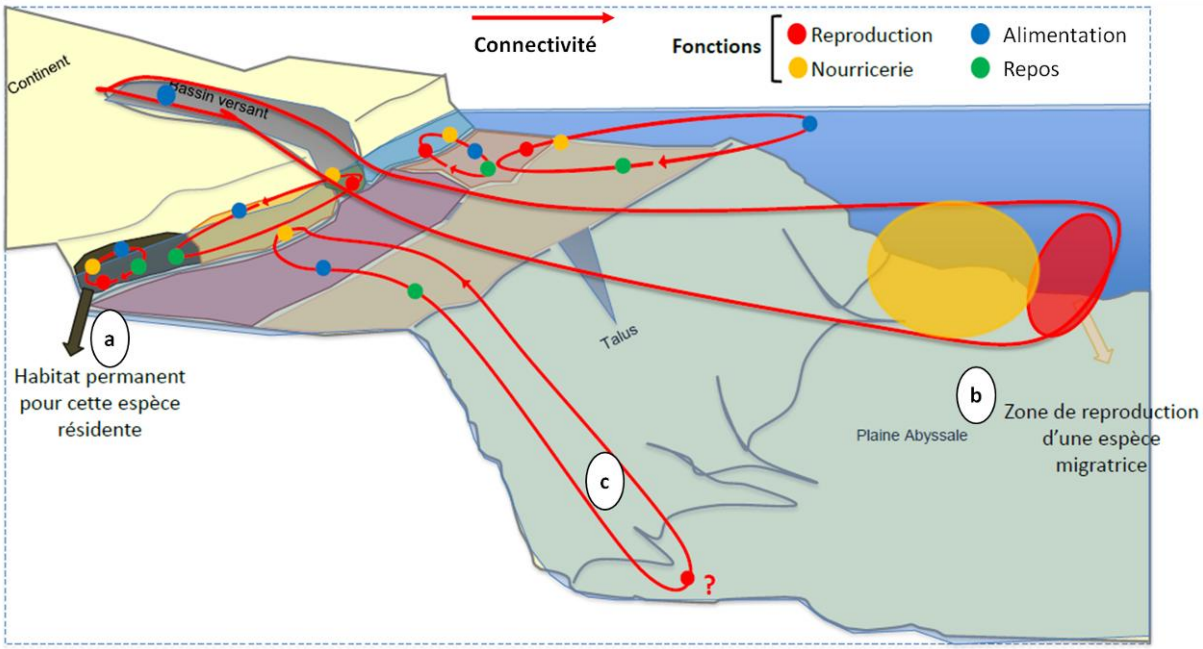

Fig. 1 : Organisation et connectivité des habitats essentiels chez les organismes marins

Dans le cas des espèces à cycle bentho-démersal comme chez de nombreux mollusques, ou des macrophytes, et certains poissons comme les gobies, les stades adultes sont sédentaires, voire fixés, tandis que la phase de dispersion s'exercera au stade larvaire. Ainsi, le plus souvent la dispersion entre les habitats essentiels et les flux de gènes entre les populations dépendront des capacités de dispersion de chacun des organismes, et de la distance séparant les habitats (Fig. 2). Plus la capacité de dispersion des organismes est forte et plus la structuration génétique sera faible. D'une manière générale, sans que cela soit une règle absolue, les organismes à cycle bentho-démersal ont une structuration relativement forte car la dispersion ne peut se faire qu'au stade larvaire représentant la phase de dispersion. A l'inverse les organismes à forte capacité de nage comme les poissons ont une capacité de dispersion à différents stades, du stade larvaire ou juvénile, jusqu'au stade adulte. La structuration génétique dépendra alors essentiellement des caractéristiques du cycle biologique : majorité de résidents (tous les habitats essentiels étant localisés dans le même écosystème) ou de migrateurs (déplacements entre les habitats essentiels au cours du cycle vital).

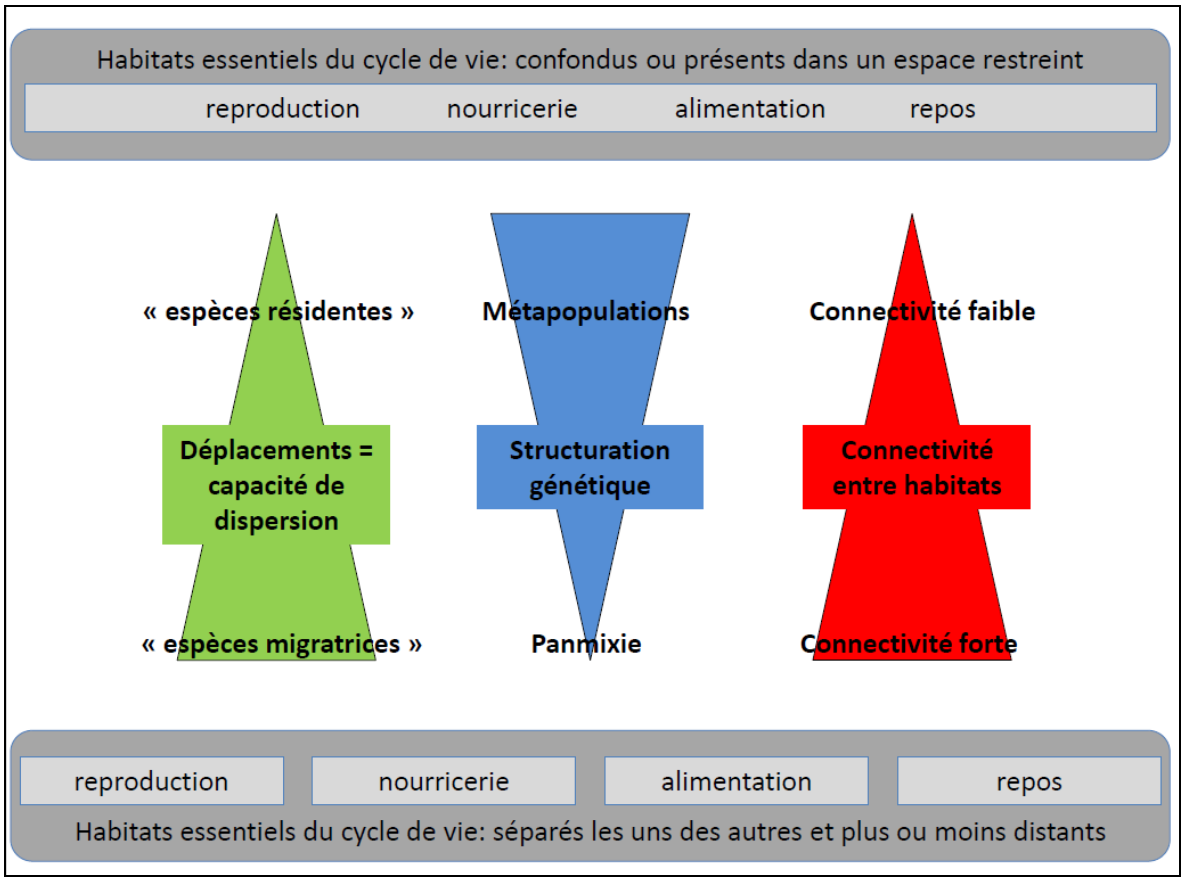

Fig. 2 : Lien entre capacité de dispersion, structuration génétique des populations et connectivité entre habitats essentiels

Vers une stratégie de protection des habitats essentiels chez les poissons à des fins de conservation.

Dans le cas des poissons, la prise en compte de certains habitats essentiels côtiers est de plus en plus importante dans la mise en œuvre des politiques de gestion. Par exemple, une réglementation internationale en Méditerranée (CGCPM) réglemente la pêche au Merlu en protégeant ses habitats de reproduction situés sur le talus continental (Fig. 1, repère c). Notamment, avec l'essor des travaux sur les habitats rocheux côtiers en Méditerranée ou des estuaires et marais salés sur les côtes de l'ouest de l'Europe, l'attention est particulièrement portée sur les habitats de nourricerie. Il s'agit premièrement de protéger différents habitats de nourricerie propres à chaque espèce d'intérêt (Fig. 3). C'est-à-dire tenir compte de la partition spatiale des juvéniles d'espèces différentes au sein de différents habitats (Harmelin-Vivien et al., 1995) due à leur complémentarité spatiale et à la synergie entre ceux-ci (e.g. « edge effect », voir Thiriet et al. (accepted)). Il faut donc savoir où et en quelle quantité se trouvent les habitats dont le rôle de nourricerie est déjà connue (Chapitre II), et de plus quelles sont les autres habitats de la mosaïque paysagère de l'Infralittoral rocheux qui jouent un rôle de nourricerie (Chapitre III) ? De plus on cherchera à protéger des portions d'habitats des adultes, à partir desquels les zones exploitées pourront être réapprovisionnées en adultes par effet spill-over (Abesamis et al., 2006; Goni et al., 2008; Grüss et al., 2011). Enfin il faut également s'assurer que les nourriceries sont présentes en nombre suffisant et à distance adéquate des habitats adultes, pour garantir une bonne connectivité entre ces habitats et permettre les migrations ontogéniques (Cheminée et al., 2011; Di Franco et al., 2012; Gillanders et al., 2003). Chaque site littoral, de par ses spécificités, requiert ainsi sa propre lecture du paysage.

En nous appuyant sur une étude de cas concrète, les nourriceries des poissons sparidés du genre *Diplodus* (sars) dans la zone du Parc national des Calanques (Marseille ; Méditerranée nord-occidentale, Fig. 4), nous montrerons que la gestion des peuplements de poissons doit se faire non seulement en développant une approche de contrôle des prélèvements mais doit aussi être complétée par une gestion de l'ensemble des habitats essentiels fréquentés lors des différents stades de vie de ces espèces. En d'autres termes, le but du présent article est 1) d'analyser si le zonage des mesures de gestion de notre cas d'étude prend en compte une approche à l'échelle du paysage et 2) de proposer un schéma conceptuel guidant le gestionnaire dans une telle approche, avec les outils dont il dispose ; cette étude de cas nous permettra de plus de proposer quelques recommandations pratiques applicables à la gestion tant réglementaire que contractuelle de l'ensemble de la zone littorale méditerranéenne.

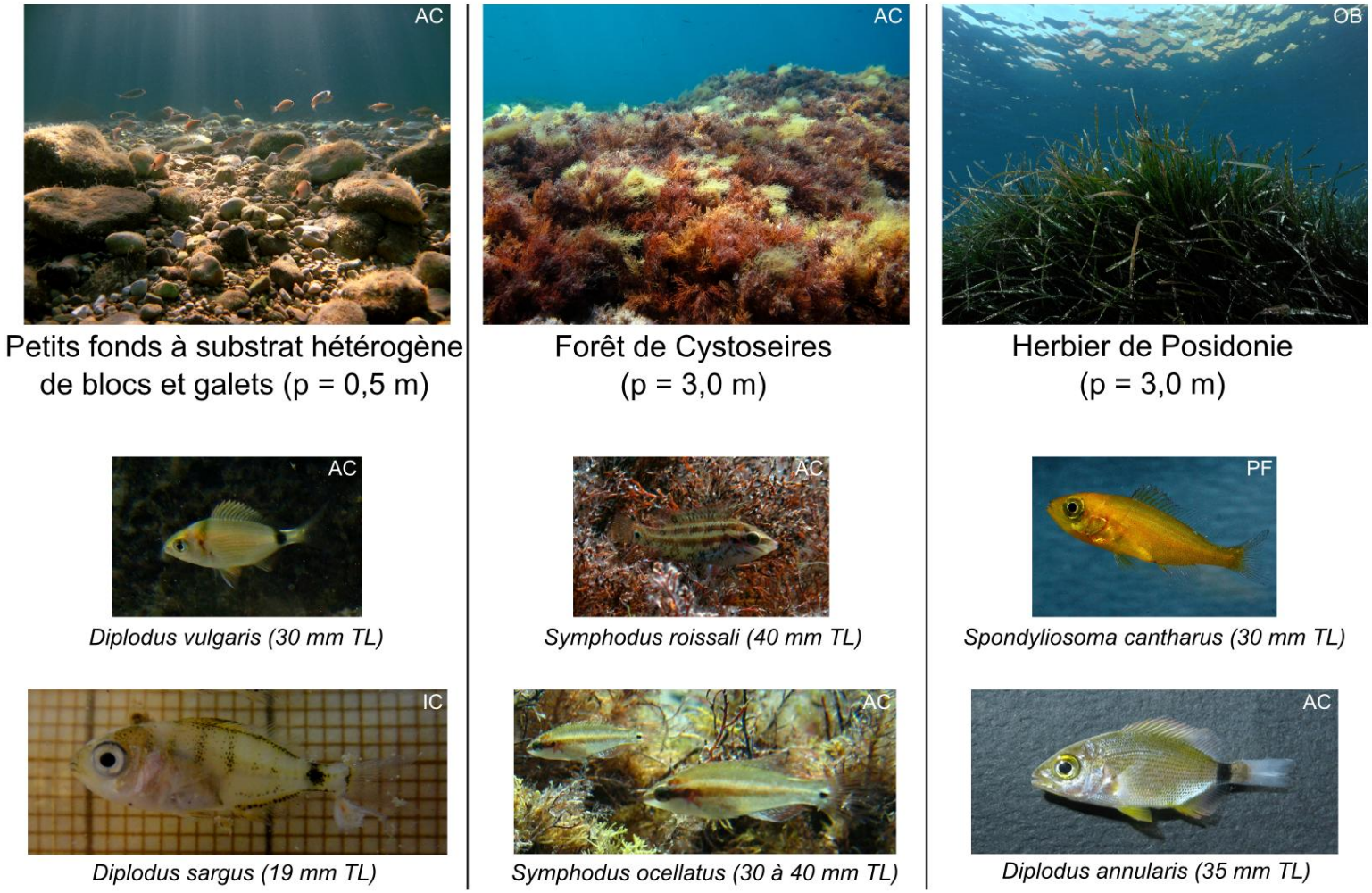

Fig. 3 : Illustrations des trois principaux habitats nourriceries le long du littoral méditerranéen (p = profondeur) et des juvéniles des espèces les plus caractéristiques (crédit photo : AC=Adrien Cheminée ; IC=Isabel Amalia Cuadros-Casado ; OB=Olivier Bianchimani ; PF=Patrice Francour)

Analyse de cas : les nourriceries de *Diplodus* spp. et le zonage du Parc National des Calanques

Les principaux enjeux :

Les espèces de poissons sparidés appartenant au genre *Diplodus* sont ciblées par les pêcheurs professionnels et amateurs, notamment en chasse sous-marine (Coll et al., 2004; Guidetti et al., 2008). Elles ont un fort intérêt économique le long des côtes méditerranéennes. Ces poissons, prédateurs d'oursins, assurent notamment un contrôle « top-down » de ces herbivores et participent donc à la prévention des phénomènes de surpâturage des fonds rocheux (Sala *et al.*, 1998). Le renouvellement de leurs peuplements est donc un enjeu autant économique qu'écologique. Les habitats jouant le rôle de nourriceries pour les juvéniles de sars *Diplodus* spp. (*Diplodus* sargus, *D. puntazzo*, *D. cervinus* et dans une moindre mesure *D. vulgaris*) sont les zones de petits fonds (0 - 1,5 mètres de profondeur), en pente douce, abritées de l'hydrodynamisme et avec un substrat hétérogène de petits blocs, galets, graviers, sables (Fig. 3). Si le substrat est constitué exclusivement de fractions fines homogènes (sable) la valeur de nourricerie de l'habitat - *sensu* Beck et al. (2001) – est sévèrement réduite (Bussotti and Guidetti, 2010; Cheminée et al., 2011; Garcia-Rubies and Macpherson, 1995; Guidetti, 2000; Harmelin-Vivien et al., 1995; MacPherson, 1998; Vigliola and Harmelin-Vivien, 2001). Dans l'exemple du site classé du Massif des Calanques de Marseille à Cassis, Cheminée et al. (2011) soulignent que les populations adultes de *Diplodus* spp. des Calanques sont probablement alimentées par des recrues migrant depuis des nourriceries situées non seulement sur place mais aussi, et en majorité, dans la Rade de Marseille, de Cassis ou de La Ciotat c'est-à-dire en dehors du site classé. Le Parc national des Calanques, officiellement créé début 2012, englobe un linéaire côtier qui s'étend de la Rade Sud de Marseille à la Baie de La Ciotat et des Lecques. Pour répondre à l'enjeu de gestion des populations de ces espèces, via la prise en compte de l'ensemble des habitats essentiels, les zonages réglementaires ou les actions de protection contractuelle devraient donc agir à une échelle spatiale qui dépasse l'habitat et se situe à l'échelle d'un paysage couvrant la moitié du linéaire côtier des Bouches-du-Rhône (Fig. 4).

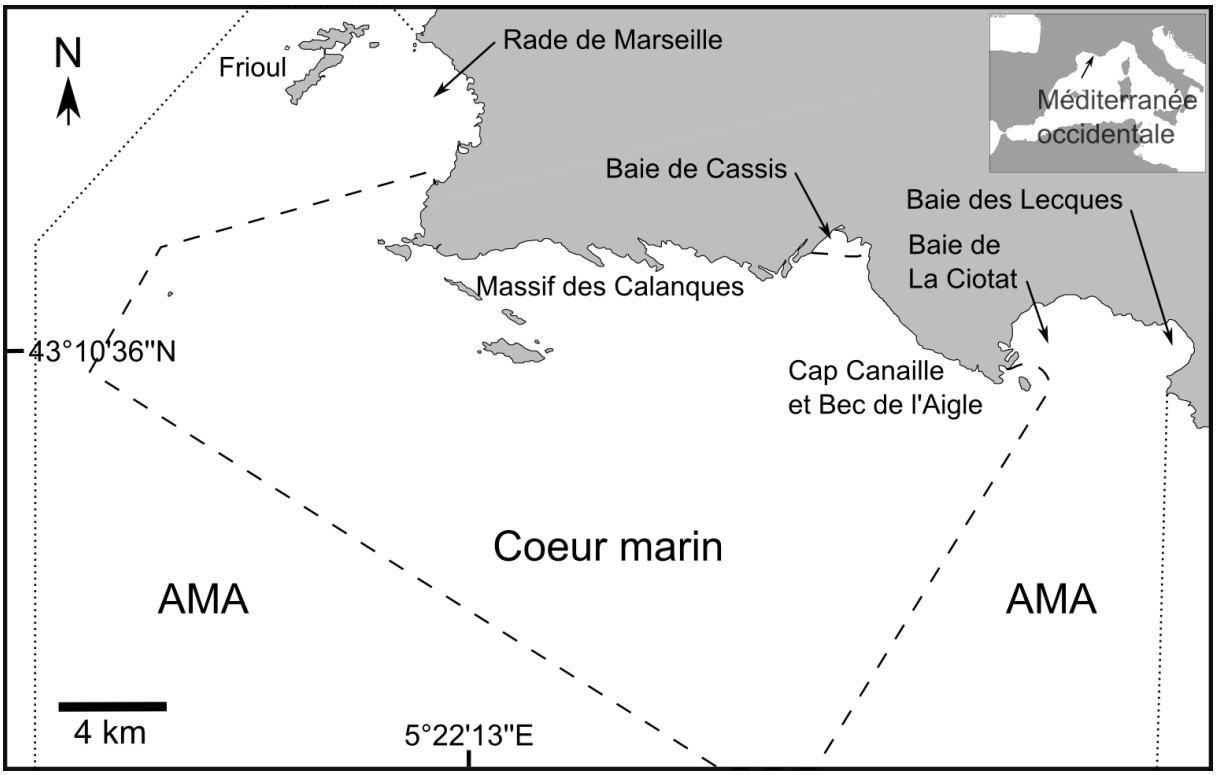

Fig. 4 : Localisation de la zone d'étude – Zonage marin du Parc national des Calanques : Cœur marin (secteurs : Massif des Calanques et Cap Canailles-Bec de l'Aigle) ; Aire Maritime Adjacente (AMA, secteurs : Rade de Marseille, Archipel du Frioul, Baie de Cassis, Baie de La Ciotat, Baie des Lecques)

Localisation des nourriceries et présentation du zonage du Parc

Sur l'ensemble du littoral du Parc national des Calanques, nous avons localisé et quantifié les portions du linéaire de côte présentant des habitats nourriceries pour les juvéniles de sars. Le littoral étudié s'étend de la Rade de Marseille (Anse de Malmousque) jusqu'à la Baie de La Ciotat – Les Lecques et inclut les Archipels du Frioul et de Riou ainsi que l'Ile Verte (Fig. 4). Il correspond à un linéaire côtier total de 151 km. Avec la même méthode que Cheminée et al. (2011) nous avons analysé les ortho-photographies de ce littoral (Google_Inc., 2011; MEDDTL et al., 2012) pour compléter la localisation des nourriceries de sars précédemment identifiées (Cheminée et al., 2011). Le linéaire côtier de chacune des nourriceries a été mesuré sur les ortho-photographies à une échelle de 1 : 7000. En plus de la vérité-terrain effectuée lors de l'étude précédente (printemps-été 2004, Rade Sud de Marseille, Calanques de Marseille à Cassis) une partie des nourriceries nouvellement identifiées sur ortho-photographies dans la Baie de La Ciotat et autour du Frioul ont été inspectées *in situ* en juillet 2008 et 2011.

Dans un second temps, le linéaire côtier a été découpé en fonction du zonage des catégories de gestion du milieu naturel existantes en région PACA et notamment sur ce secteur et répertoriées sur le site Internet de la DREAL (DREAL_PACA, 2012; GIP_Calanques, 2012) : protections réglementaires, protections contractuelles et inventaires patrimoniaux. Sur le

zonage du Parc national des Calanques (Fig. 4) on distingue notamment (1) le cœur marin qui contient deux secteurs, le Massif des Calanques (dont l'archipel de Riou) et le secteur du Cap Canaille et Bec de l'Aigle (dont l'île Verte) et (2) l'Aire Maritime Adjacente (AMA) qui englobe la Rade Sud de Marseille, le DPM (Domaine public maritime) autour de l'archipel du Frioul et les baies de Cassis, La Ciotat et des Lecques. La box 1 détaille les types de protections du Parc.

Le linéaire côtier présentant des habitats nourriceries et la proportion du trait de côte total qu'elles représentent ont été calculés pour chaque catégorie de protection réglementaire et contractuelle du Parc (Table 1).

Box 1 : Protections réglementaires et contractuelles du Parc national des Calanques

Le cœur de Parc comporte une réglementation « spéciale cœur » applicable sur toute son étendue, incluant par exemple en ce qui concerne les ressources marines l'interdiction du chalutage et de la pêche au gangui. Le statut de cœur implique de plus un principe d'interdiction de travaux, construction, installation, sauf autorisation dérogatoire. Plus ponctuellement, des zones de non prélèvement ou de protection renforcée (ZNP et ZPR) présentent un niveau de protection plus élevé que la moyenne du cœur. Pour tous les autres aspects réglementaires (par exemple les tailles de captures), la compétence en revient aux autorités administratives habituellement en exercice en mer (Préfet, …). En revanche l'établissement public Parc a la possibilité de faire des propositions de (nouvelles) réglementations à ces autorités compétentes. En ce qui concerne l'aire maritime adjacente (AMA), la protection apportée par le Parc y est uniquement contractuelle : de manière générale aussi bien pour le cœur que pour l'AMA, la charte de Parc introduit en effet la possibilité de mettre au point des mesures de protection partenariales (sur le modèle par exemple des Parc naturels régionaux ou des contrats Natura 2000).

Les nourriceries à l'épreuve du zonage du Parc national des Calanques

La table en Annexe 1 de cet article présente la liste de l'ensemble des nourriceries de *Diplodus* spp. trouvées dans le périmètre du Parc national des Calanques et quantifie le linéaire de côte correspondant (en mètres). La figure 5 en donne une représentation cartographique permettant de les localiser précisément[16]. Les habitats nourriceries de *Diplodus* spp. occupent seulement 7,2 % des 151 km de linéaire côtier de l'ensemble du Parc national (Table 1). Au total, 62% de ces nourriceries sont situées dans l'AMA et 38 % dans le cœur. Autrement dit, au sein du cœur, ces habitats nourriceries n'occupent que 5,3 % du linéaire côtier contre 9 % au sein de l'AMA. Il est notable que seuls 2 % des nourriceries du cœur sont incluses dans la catégorie « zones de non prélèvement » (ZNP) et 0% en ZPR. Dans le cœur le seul type de protection contractuelle en finalisation à ce jour est la catégorie « Natura 2000 » : ceci concerne l'ensemble du cœur et donc 100 % des nourriceries du cœur. Au sein de l'AMA, la seule catégorie de protection réglementaire présente correspond à des portions du « site classé » : seuls 13% des nourriceries de l'AMA sont couvertes par cette catégorie. Parmi les mesures partenariales qui pourront être mise en place dans l'AMA, la catégorie de protections contractuelles déjà existante sur au moins une partie de l'AMA est « Natura 2000 » (en voie de finalisation) et concerne 32% des nourriceries de l'AMA. Les 68 % restant de nourriceries de l'AMA ne bénéficient pas pour l'heure de protection contractuelle particulière. Par ailleurs, en termes d'inventaire du patrimoine naturel, 41 % des nourriceries du Parc sont incluses dans une ZNIEFF marine (I ou II). Cinquante-sept pourcents des nourriceries du cœur appartiennent à une ZNIEFF alors que seulement 31% des nourriceries de l'AMA appartiennent à cette catégorie.

[16] See also Chapter V-part 3 for the full Atlas

Table 1. Zonage – types et catégories de gestion existantes en région PACA et sur le territoire d'étude : protections réglementaires, contractuelles et inventaires applicables au milieu marin et considérés dans cette étude (DREAL_PACA, 2012) – linéaire de côte, linéaire de nourriceries et proportions correspondantes

Type de protection	Catégories	Linéaire de côte (m)	Linéaire de nourriceries (m)	Proportion de l'ensemble des nourriceries du Parc national	Linéaire de nourriceries du cœur (m) appartenant à cette catégorie	Proportion des nourriceries du cœur appartenant à cette catégorie	Linéaire de nourriceries de l'AMA appartenant à cette catégorie	Proportion des nourriceries de l'AMA appartenant à cette catégorie
Protection réglementaire	**Cœur marin** (réglementation générale spéciale cœur)	**76425**	4076	**38**	4076	**100**	-	**-**
	ZNP et ZPR du Cœur (Zone de Non Prélèvement et de Protection Renforcée)		81	**1**	81	**2**	-	**-**
	Site classé		4925	**46**	4076	**100**	849	**13**
Protection contractuelle	**Aire Maritime Adjacente** (mesures partenariales à proposer)	**74584**	6745	**62**	-	**-**	6745	**100**
	Site Natura 2000		6244	**58**	4076	**100**	2168	**32**
Inventaires du patrimoine	**ZNIEFF-mer I** (Zone d'Intérêt Ecologique Faunistique et Floristique)		2266	**21**	2266	**55**	0	**0**
	ZNIEFF-mer II (Zone d'Intérêt Ecologique Faunistique et Floristique)		2178	**20**	66	**2**	2112	**31**
	Total ZNIEFF-mer		4444	**41**	2332	**57**	2112	**31**
Ensemble du Parc national		**151009**	**10821**					

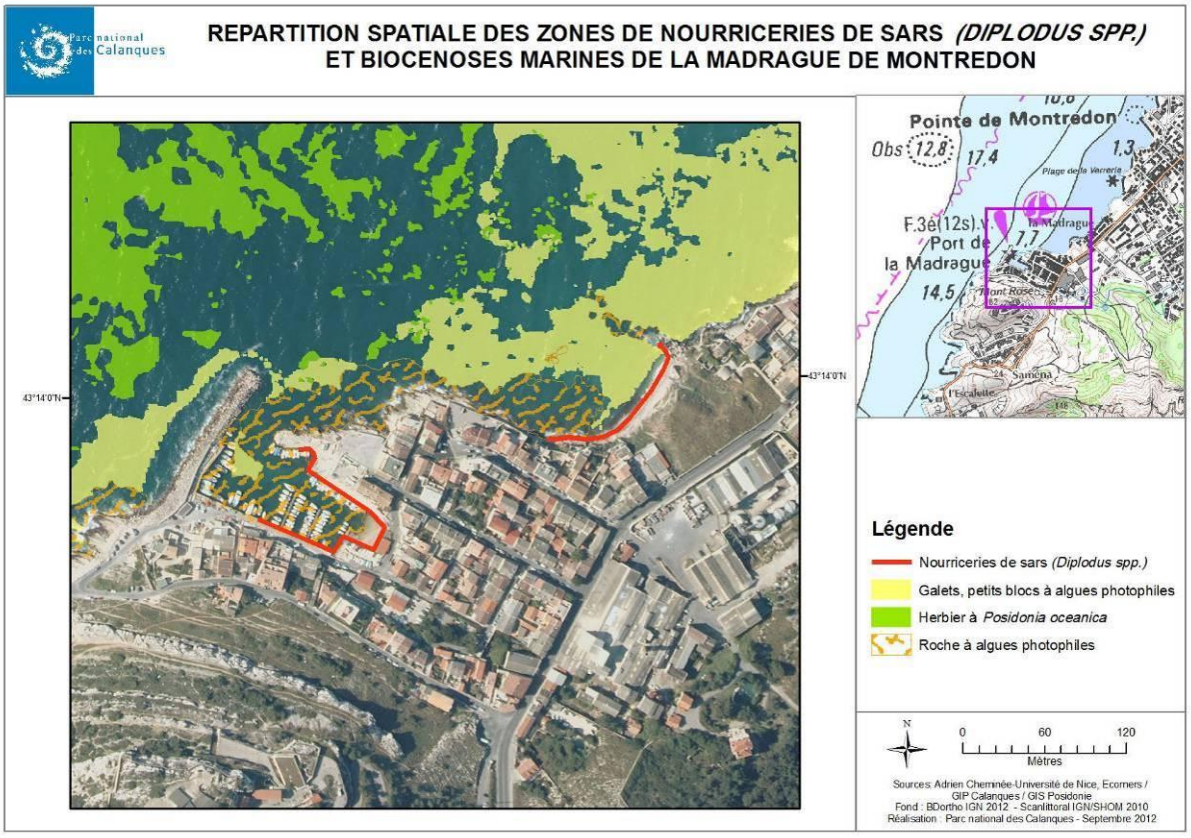

Fig. 5 : Carte de localisation des nourriceries – extrait de l' « Atlas des zones de nourriceries de sars (*Diplodus* spp.) et biocénoses marines du Parc National des Calanques » (in prep.)[17]. Zone de la Madrague de Montredon (Rade de Marseille, cf. Fig. 4).

Discussion : appliquer l'approche paysage en termes de gestion de l'Infralittoral

Sur l'ensemble du territoire du Parc national des Calanques, la quantité de nourricerie de *Diplodus* spp. est faible (moins de 8% du linéaire côtier total). De plus, la plus grande partie de ces nourriceries se situent hors du cœur, dans l'AMA, où d'une part les pressions anthropiques sont élevées (rades de Marseille et La Ciotat) et où le niveau de protection est par définition plus faible (cf. Box 1). Ces données confirment donc celles de Cheminée et al. (2011) : les nourriceries de sars du cœur du Parc national des Calanques semblent insuffisantes pour assurer à elles seules le renouvellement des populations adultes locales et celles-ci dépendent probablement de la migration de recrues venant des nourriceries, plus abondantes, situées dans l'Aire Maritime Adjacente.

Le zonage de gestion de notre zone d'étude ne prend donc *a priori* pas en compte l'ensemble des habitats essentiels et leurs connectivités (approche « paysage »). Il existe pourtant des exemples de gestion des milieux naturels qui adoptent cette réflexion à

[17] See Chapter V-part 3 for the full Atlas

l'échelle du paysage et notamment la notion de connectivité : le concept des « solidarités écologiques » reprend ces principes et fait l'objet d'une réflexion actuelle au sein de l'établissement public Parcs Nationaux de France (Gabrié et al., 2007; INEA et al., 2009; Thompson et al., 2009). La convention de Ramsar (1971) et les recommandations des différentes Conférences des Parties qui se sont succédées ont également incités ses membres à tenir compte de la fonctionnalité des habitats et des processus de connectivité, à l'échelle du paysage, pour la sélection de leurs « zones humides d'importance internationale » (Cheminée, 2002; Direction de l'Agriculture de Mayotte et al., 2002).

Nous proposons donc ici un **schéma conceptuel** (Fig. 6) illustré par notre cas d'étude et applicable de manière générale à la gestion de tout site littoral pour en favoriser une approche « paysage ».

On cherche à gérer premièrement les habitats des juvéniles (Fig. 6, repère a). Pour cela, une fois que les caractéristiques des habitats des juvéniles (nourriceries) sont connues (b) leur cartographie (c) permet de les localiser et de les quantifier. En zone protégée réglementairement (le cœur de Parc dans notre exemple ; d) il faut veiller à la conservation de la valeur de nourricerie de l'habitat : ceci nécessite en particulier (e) le strict maintien des caractéristiques du micro-habitat ; dans le cas des sars (*Diplodus*) il a été montré (Cheminée et al., 2011) que le respect du caractère hétérogène des petits fonds en pente douce est nécessaire pour qu'ils remplissent leur fonction de nourricerie (notion d'« hétérogénéité » et de « complexité », *sensu* August (1983) [18]). Dans notre cas d'étude, les nourriceries situées dans le cœur bénéficient d'un niveau de protection élevé : la réglementation spéciale cœur et le statut de site classé impliquent un principe d'interdiction de travaux, construction et installation, affectant notamment le DPM (domaine public maritime), sauf autorisation dérogatoire, ce qui donne les moyens à l'établissement public de protéger ces habitats d'une destruction directe. Dans certains cas, si les protections réglementaires sont insuffisantes (f) l'établissement public gestionnaire peut proposer notamment (g) des mesures réglementaires complémentaires : par exemple lister spécifiquement les habitats et leurs caractéristiques devant être protégés, par exemple lors de l'accord de dérogations pour des travaux sur le DPM de la zone cœur. Une fois cette étape passée, il faut s'assurer (h) que les nourriceries sont connectées aux habitats adultes et présentes en quantités suffisantes pour en assurer l'alimentation en recrues. Dans notre exemple, comme mentionné précédemment, les nourriceries des Calanques ne sont pas présentes en quantité suffisante dans le cœur (i) : les habitats adultes du cœur dépendent alors (j) majoritairement de migration de recrues venant des nourriceries distantes, situées hors zone protégée réglementairement c'est-à-dire, dans notre exemple, dans l'AMA. Il est donc nécessaire d'y appliquer le même raisonnement : dans l'AMA on a constaté ci-dessus que 3/5 des

[18] See a detailed definition in Chapter VI-general discussion

nourriceries ne bénéficient d'aucune protection réglementaire ou contractuelle spécifique. L'intégrité de ces habitats (maintien de leurs caractéristiques) et donc de leur valeur de nourricerie (k) dépend donc fortement du processus de contractualisation à venir (l), qui définira par concertation les actions de gestion (mesures partenariales) dans l'AMA. Par exemple, dans le cas des sars, en application du principe d'hétérogénéité mentionné précédemment, il y a un travail de sensibilisation a effectuer aussi bien auprès des décideurs que de la société civile pour les encourager, par voie contractuelle, à préserver des plages naturelles, disposant d'un substrat hétérogène et ne plus vouloir systématiquement re-profiler ces plages ou les engraisser exclusivement de fractions fines. Il s'agit là d'une nécessaire conciliation entre enjeux environnementaux et enjeux économiques liés aux activités balnéaires. Une fois de telles garanties acquises (k), cette approche « paysage » de la gestion nécessite là encore (m) le maintien de la connectivité entre nourriceries situées hors zone protégée et habitats adultes : la faisabilité de telles migrations de jeunes recrues de sars est confirmée par des travaux récents (Di Franco et al., 2012) démontrant la capacité des recrues à migrer depuis les nourriceries vers les habitats adultes sur des distances de 10 à 30 km. De plus, il est nécessaire de disposer d'une quantité suffisante de nourriceries (m). Si ce n'est pas le cas, deux options peuvent être envisagées, aussi bien en zone protégée que non protégée réglementairement : premièrement, les causes de ce manque de nourriceries peuvent être actuelles (n), par exemple si elles ont été partiellement dégradées suites à des pollutions (altération des forêts de Cystoseires) ou re-profilage des plages (altération des petits fonds hétérogènes à blocs). Dans ce cas, le gestionnaire peut envisager des mesures de restauration (o) pour rétablir les caractéristiques des micro-habitats et donc la valeur de nourricerie de ces habitats. Ou alors, les causes de ce manque de nourriceries peuvent être historiques (p) et irrémédiables, par exemple en cas de destructions par des aménagements portuaires (voir détails en Box 2) ; des mesures de compensation peuvent alors être envisagées pour remplacer ces nourriceries perdues (q). Au terme de ce raisonnement, aussi bien en zone protégée que non protégée réglementairement, une fois que les nourriceries de chaque espèce d'intérêt ont été identifiées (caractéristiques), localisées (cartographie) et que leur quantité et leur connectivité avec les habitats adultes sont satisfaisantes et préservées, l'étape suivante consiste à se préoccuper de la gestion des populations adultes elles-mêmes (r) ; dans notre cas d'étude, au sein du cœur, outre la réglementation générale en mer (respect des tailles de captures, etc.), la réglementation spéciale cœur et les zones de non prélèvements (ZNP et ZPR) permettent de gérer l'habitat et les populations des adultes. En zone adjacente (AMA) des opérations comme les récifs artificiels de la baie du Prado y participent également.

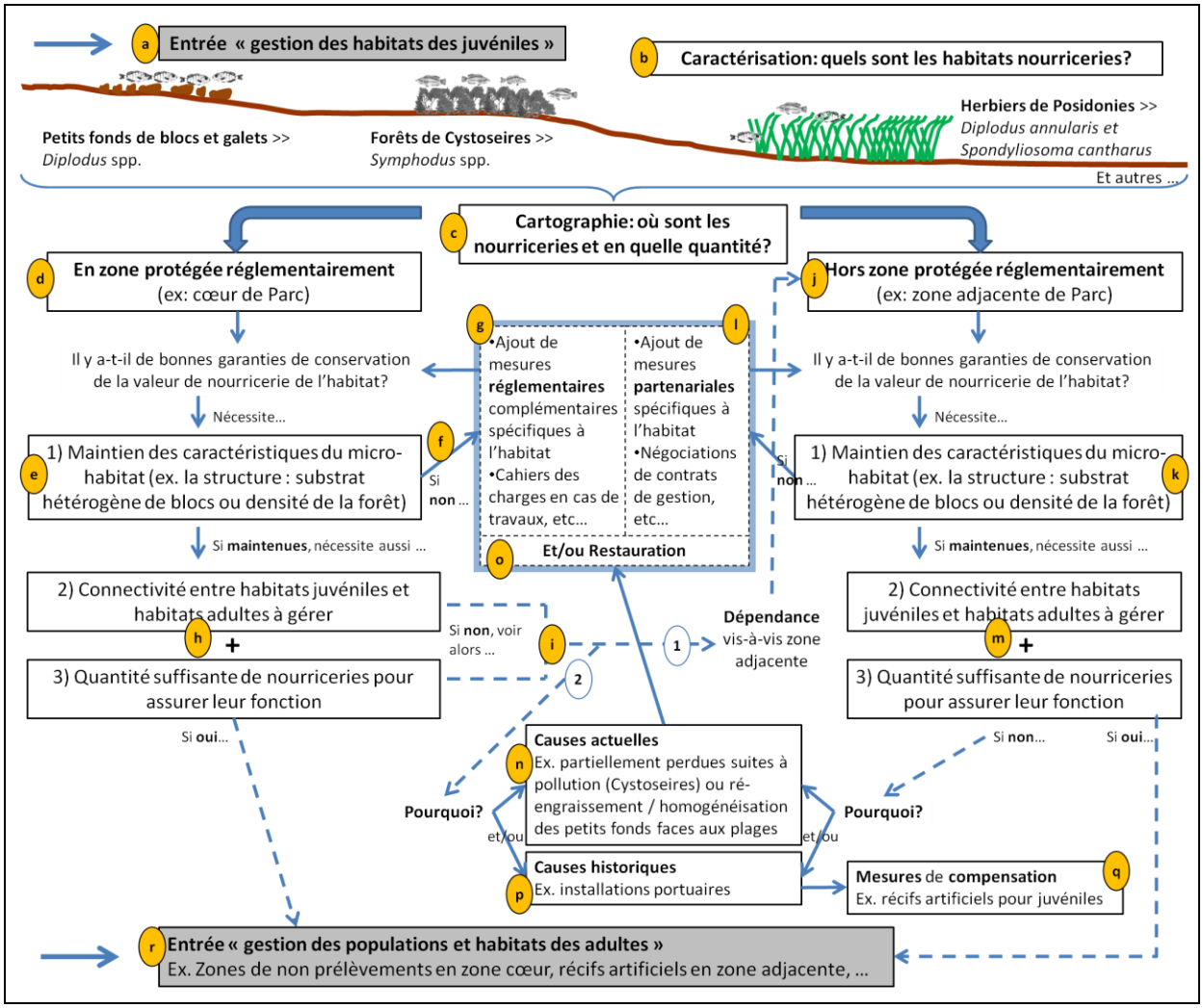

Fig. 6 : Schéma conceptuel pour une approche « paysage » de la gestion des zones côtières

Box 2 : Causes historiques : cas des grands aménagements littoraux du 19ième et 20ième siècle en Rade de Marseille

En Rade de Marseille (c.à.d. pour partie dans l'AMA), quelle est la productivité qui a été perdue par la destruction irrémédiable des nourriceries qui étaient situées à l'emplacement actuel des grands aménagements littoraux du 19ième et 20ième siècle ? Selon Meinesz et al. (2006), sur la commune de Marseille, avant l'essentiel de l'artificialisation des côtes (c'est-à-dire avant 1800) le linéaire côtier initial était de 114 km ; 32 km de linéaire côtier ont été artificialisés, aboutissant à un taux d'occupation des petits fonds (0-10 mètres) de 49 % de leur surface initiale (1421 ha). Par exemple, les plages alvéolaires artificielles aménagées au Prado (Prado-Plage et Prado Bonneveine, Annexe 1) sont constituées d'un substrat homogène de graviers fin, et séparées par des enrochements massif et abrupts. Ces aménagements ont été réalisés (fin des années 1970) par-dessus des zones de petits fonds incluant des zones de nourriceries de sars c'est-à-dire les fonds à granulométrie hétérogène à petits blocs et graviers. Cette destruction et homogénéisation des habitats a probablement fortement réduit la quantité de nourricerie de la Rade de Marseille. Elles ont artificialisé 3152 mètres de côte (Meinesz et al., 2006). Compte tenu de la quantité de nourriceries présentes actuellement sur une zone témoin peu artificialisée (Montredon, Annexe 1, Fig. 5) on peut estimer que les nourriceries occupaient environ 50% du linéaire côtier du Prado, soit 1576 mètres. Il n'en subsiste aujourd'hui que 372 m (Annexe 1), soit une perte que nous estimons à plus de 75%. Il en est de même pour la zone du Port Autonome de Marseille (Rade Nord de Marseille) : l'examen des anciennes cartes d'Etat Major (Fig. 7) élaborées de 1825 à 1866 (MEDDTL et al., 2012) indique que la côte à l'emplacement des bassins du Port Autonome avait une morphologie propice à la présence de nourriceries de sars. Cet ouvrage construit de 1844 à 1975 a occasionné l'artificialisation d'un total de 11533 mètres de littoral (Meinesz et al., 2006), modifiant des habitats qui ont irréversiblement perdu leur fonction de nourricerie étant donné la transformation radicale de leur morphologie (quais abruptes et profondeur importante). Nous estimons que cette côte présentait également des nourriceries sur 50% de son linéaire, et que celles-ci alimentaient les habitats adultes de l'actuel Parc Marin de la Côte Bleue, situé à une douzaine de kilomètres à l'Ouest du Port, et qui ne présente que peu de nourricerie à l'instar du cœur du Parc national des Calanques. L'impact qu'on eu ces transformations est donc considérable.

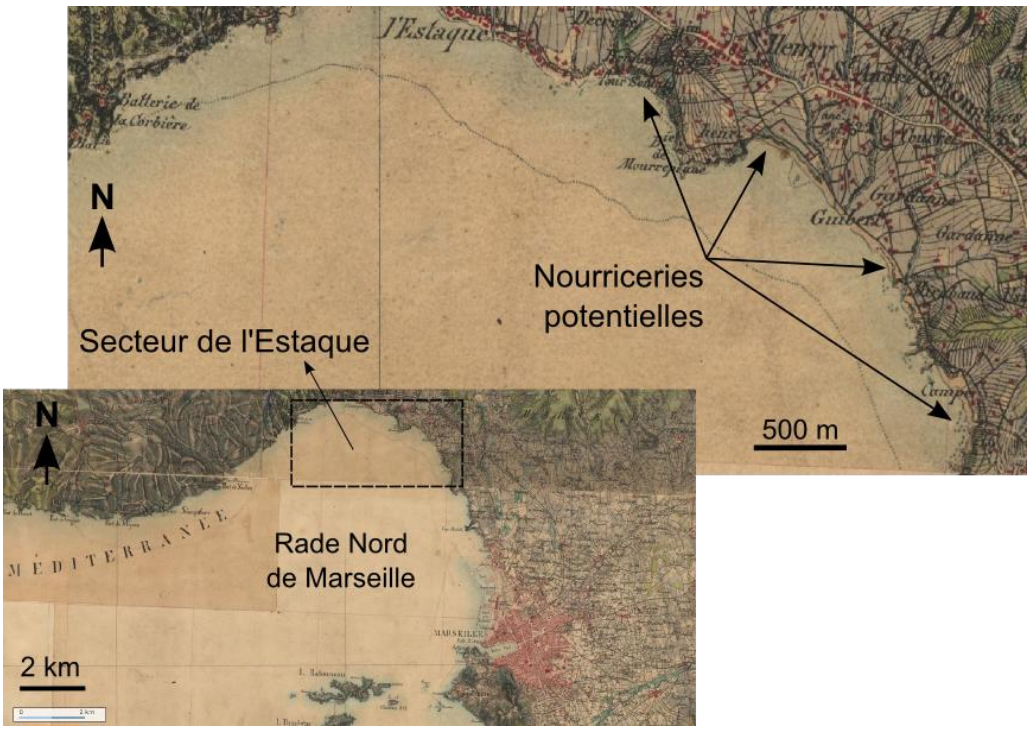

Fig. 7 : Extrait des cartes d'Etat Major (1825-1866). Rade Nord de Marseille, secteur de l'Estaque – Exemples d'anciennes zones d'habitats nourriceries détruites par les aménagements portuaires de l'actuel Port Autonome – Source : IGN – Géoportail

Perspectives de gestion : quels moyens d'actions ?

L'application de cette « approche paysage » de la gestion passe par la réalisation d'un plan d'actions : en termes de recommandations pratiques pour le gestionnaire, on retiendra notamment que des aménagements littoraux non concertés qui homogénéisent l'environnement à chacune de ses échelles (du micro-habitat au paysage entier) sont donc néfastes notamment pour le rôle de nourricerie des zones côtières. A l'inverse, des aménagements réfléchis, adaptés au cas par cas pour maintenir la valeur de nourricerie des zones côtières, peuvent être envisagés. Ces notions théoriques doivent être intégrées en pratique à la gestion réglementaire et contractuelle du littoral. La Box 3 en donne une illustration pour notre cas d'étude. Globalement il faudra notamment (1) maintenir et protéger une mosaïque d'habitat variés aussi bien à l'échelle d'une crique qu'à l'échelle d'une baie entière pour garantir la complémentarité des habitats pour différentes espèces ou les différentes étapes du cycle de vie d'une espèce donnée ; (2) respecter la morphologie de ces habitats essentiels : en ce qui concerne les aménagements littoraux (e.g. portuaires), le bien fondé de certains travaux est ainsi à repenser à la lumière de ces perspectives et des solutions alternatives évitant une transformation radicale de l'habitat doivent être discutées.

Box 3 : Les moyens d'application d'une « approche paysage » de la gestion – cas du Parc National des Calanques

Afin de mettre en œuvre de telles recommandations, divers moyens d'actions sont à la disposition de l'établissement public du Parc National des Calanques. Notamment, (1) sur le plan des mesures de protection, l'établissement public a le devoir d'émettre des propositions de mesures réglementaires aux autorités compétentes. Parallèlement la charte introduit la possibilité de proposer des mesures partenariales. Ces deux outils pourraient être utilisés pour mettre en place des mesures de protection qui soient spécifiques aux habitats essentiels, notamment les nourriceries de sparidés ; c'est-à-dire qui stipulent explicitement la volonté et les moyens de préserver leurs caractéristiques biotiques et abiotiques. En effet, à la lecture des mesures partenariales du projet de charte, on remarque que la notion de paysage est employée mais qu'elle reste relativement générale. De futures propositions de mesures complémentaires pourraient être l'occasion de définir précisément certains habitats à enjeux élevés, qui ne sont actuellement pas individualisés sur les cartographies des biocénoses type « Natura 2000 », et qui n'ont jusqu'à présent pour ainsi dire pas été pris en considération dans les plans de gestion. C'est le cas par exemple les petits fonds hétérogènes nourriceries. Par ailleurs, (2) en zone cœur, l'instruction des demandes de dérogations à l'interdiction de travaux/construction/installation devra prendre en compte les recommandations mentionnées précédemment. De plus, sur une zone de nourricerie donnée, les éventuelles dérogations accordées, par exemple du fait que le projet de travaux considéré ne produit pas une destruction des habitats, devront néanmoins spécifier dans le cahier des charges quelles sont les caractéristiques du micro-habitat qui doivent elles aussi être conservées. Enfin, (3) sur le plan foncier, il pourrait être demandé une réaffectation du DPM situé au droit des terrains du Conservatoire du littoral (CELRL), afin de transférer les compétences administratives du préfet de département (DDTM) vers le Conservatoire et le Parc. Ceci fournirait au Parc un levier supplémentaire de gestion des habitats et faciliterait alors une adéquation et une application coordonnée des mesures de gestion à l'échelle des paysages sous-marins.

Remarque sur les aménagements portuaires – Des ports dimensionnés comme ceux des Goudes ou de Morgiou (faible hauteur de quai, conservation de la nature hétérogène des fonds) leur permettent de conserver une haute valeur de nourricerie, à l'opposé des bassins profonds et uniformes du port autonome par exemple. Un désensablement/approfondissement est-il systématiquement nécessaire pour ces ports ? Des solutions alternatives, évitant une transformation radicale de l'habitat, doivent être discutées.

Remerciements

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Annexe 1. Les nourriceries de *Diplodus* spp. au sein du Parc national des Calanques - zonage, secteurs (cf Fig. 4) et linéaire côtier correspondant (mètres) – Il est précisé pour chaque nourricerie si son identification provient de la seule interprétation des ortho-photos aériennes (O) ou si celle-ci a été confirmée *in situ* par une visite de « vérité terrain » (T)

Nourriceries (nom du lieu-dit)	Zonage du Parc	Secteur	Ortho-photo (O) ou vérité terrain (T)	Linéaire (m)
Port de Malmousque	AMA	Rade de Marseille	**T**	**113**
Quai des Légionnaires	AMA	Rade de Marseille	**T**	**84**
Plage des Légionnaires	AMA	Rade de Marseille	**O**	**31**
Plage Cadière	AMA	Rade de Marseille	**O**	**28**
Anse aux Cuivres bis	AMA	Rade de Marseille	**T**	**14**
Anse aux Cuivres	AMA	Rade de Marseille	**T**	**49**
Plage Station marine	AMA	Rade de Marseille	**T**	**26**
Anse de Maldormé	AMA	Rade de Marseille	**T**	**50**
Plage du Prophète	AMA	Rade de Marseille	**T**	**93**
Base de loisirs du Roucas blanc	AMA	Rade de Marseille	**O**	**481**
Prado-Plage du Grand Roucas	AMA	Rade de Marseille	**O**	**37**
Prado-Plage de David	AMA	Rade de Marseille	**O**	**43**
Prado-Plage de l'Huveaune	AMA	Rade de Marseille	**O**	**51**
Prado-Plage Borély	AMA	Rade de Marseille	**O**	**177**
Prado-Plage Bonneveine	AMA	Rade de Marseille	**O**	**64**
Plage Vieille Chapelle	AMA	Rade de Marseille	**O**	**118**
Plage de la Pointe Rouge	AMA	Rade de Marseille	**O**	**428**
Montredon-Anse des Phocéens et Piscine	AMA	Rade de Marseille	**T**	**184**
Montredon-Anse des Sablettes sud et nord	AMA	Rade de Marseille	**T**	**219**
Montredon-Verrerie sud et nord	AMA	Rade de Marseille	**T**	**188**
Montredon-La Madrague plage	AMA	Rade de Marseille	**T**	**124**
Port de la Madrague	AMA	Rade de Marseille	**T**	**181**
Frioul-port de pomègues	AMA	Archipel Frioul	**O**	**122**
Frioul-calanque de la Crine	AMA	Archipel Frioul	**T**	**94**
Frioul-plage pompiers	AMA	Archipel Frioul	**O**	**50**
Frioul-calanque Morgiret	AMA	Archipel Frioul	**O**	**136**
Frioul-calanque du Berger	AMA	Archipel Frioul	**O**	**10**
Frioul-Eoube	AMA	Archipel Frioul	**O**	**64**
Frioul-calanque de Ratonneau	AMA	Archipel Frioul	**O**	**28**
Frioul-calanque de St-Estève	AMA	Archipel Frioul	**T**	**133**
Frioul-plage des Pilotes	AMA	Archipel Frioul	**O**	**19**
Frioul-port	AMA	Archipel Frioul	**O**	**513**
Samena	Cœur	Rade de Marseille	**T**	**22**
Mauvais Pas	Cœur	Rade de Marseille	**T**	**53**
Escalette	Cœur	Rade de Marseille	**T**	**75**
Blanche	Cœur	Rade de Marseille	**T**	**11**
Port des Goudes	Cœur	Rade de Marseille	**T**	**437**
Maronaise	Cœur	Rade de Marseille	**T**	**35**

Baie des Singes (port)	Cœur	Massif des Calanques	**T**	**94**
Maire Est	Cœur	Massif des Calanques	**T**	**27**
Callelongue entrée	Cœur	Massif des Calanques	**T**	**15**
Callelongue interne	Cœur	Massif des Calanques	**T**	**144**
Monasterio plage	Cœur	Massif des Calanques	**T**	**44**
Mounine	Cœur	Massif des Calanques	**T**	**12**
Marseilleveyre	Cœur	Massif des Calanques	**T**	**105**
Queyrons	Cœur	Massif des Calanques	**T**	**36**
Podestat	Cœur	Massif des Calanques	**T**	**37**
Sormiou	Cœur	Massif des Calanques	**T**	**316**
Morgiou	Cœur	Massif des Calanques	**T**	**396**
Sugiton	Cœur	Massif des Calanques	**T**	**79**
Pierres tombées	Cœur	Massif des Calanques	**T**	**206**
Envau	Cœur	Massif des Calanques	**T**	**67**
Port-Pin	Cœur	Massif des Calanques	**T**	**65**
Port-Miou	Cœur	Massif des Calanques	**O**	**982**
Baie de Cassis-plage Bestouan	AMA	Baie de Cassis	**O**	**34**
Baie de Cassis-portion du port	AMA	Baie de Cassis	**O**	**100**
Baie de Cassis-Plage du Corton	AMA	Baie de Cassis	**O**	**208**
Baie de Cassis-Anse de l'Arène	AMA	Baie de Cassis	**O**	**565**
Falaises de Soubeyrannes	Cœur	Cap Canaille-Bec Aigle	**O**	**427**
Figuerolles	Cœur	Cap Canaille-Bec Aigle	**O**	**66**
Petit Mugel	Cœur	Cap Canaille-Bec Aigle	**T**	**105**
Grand Mugel	Cœur	Cap Canaille-Bec Aigle	**T**	**109**
Ile verte	Cœur	Cap Canaille-Bec Aigle	**T**	**111**
Baie de la Ciotat-Plage de la Clinique	AMA	Baie de la Ciotat	**O**	**98**
Baie de la Ciotat-Port des Capucins	AMA	Baie de la Ciotat	**O**	**193**
Baie de la Ciotat-Plage des Capucins	AMA	Baie de la Ciotat	**O**	**64**
Baie de la Ciotat-Plages de Villa des Tours	AMA	Baie de la Ciotat	**O**	**60**
Baie de la Ciotat-Plage Lumière	AMA	Baie de la Ciotat	**O**	**16**
Baie de la Ciotat-Port de St Jean	AMA	Baie de la Ciotat	**O**	**271**
Baie de la Ciotat-Plage d'Arène Cros	AMA	Baie de la Ciotat	**O**	**61**
Baie de la Ciotat-Le Liouquet	AMA	Baie de la Ciotat	**O**	**92**
Baie de la Ciotat-Plage du Liouquet	AMA	Baie de la Ciotat	**O**	**356**
Baie de la Ciotat-Le Galand	AMA	Baie de la Ciotat	**O**	**131**
Baie des Lecques-plage du Nouveau port	AMA	Baie des Lecques	**O**	**82**
Baie des Lecques-Vieux port des Lecques	AMA	Baie des Lecques	**O**	**291**
Baie des Lecques-plage La Madrague	AMA	Baie des Lecques	**O**	**95**
Baie des Lecques-plage Anatole Ducros	AMA	Baie des Lecques	**O**	**76**
Total linéaire nourriceries (mètres)				**10821**

5.3 Supplementary data: transfer of essential habitat data to managers

5.3.1 Foreword: wishing to link research and management

Before working on this PhD thesis, I participated in various projects led by (mostly tropical-) coastal managers; they aimed at gathering existing data about the spatial distribution of essential marine habitats and incorporate them in the design of coastal management plans or coastal development programs: coastal wetlands such as seagrass meadows and mangroves, fringing coral reefs (Cheminée, 2002; Direction de l'Agriculture de Mayotte et al., 2002; Gabrié et al., 2007; Oberlinkels et al., 2007).

More recently, during my PhD, I aimed at adopting the same approach with my own data about Mediterranean essential habitats in an attempt to provide managers with useful data to better target conservation actions. For that purpose, we undertook several collaborations with, for instance, the management team of Scandola Natural Reserve that led to the results presented in Chapters III and IV. Data gathered during these works were transferred to the manager J.-M. Dominici, who presented them during a congress of Mediterranean coastal managers held in 2010. Results in the present part are the outcome of an ongoing collaboration I developed with the Calanques National Park (Marseilles, France) management team and include a cartographic atlas (**5.3.2**) of 1) the spatial distribution of infralittoral biocenosis (manager's data: previously performed "Natura 2000" cartography) along with 2) my own data of *Diplodus* spp. nursery habitat spatial distribution along the Calanques shoreline (see original data in part 5.2).

As highlighted by Beck et al. (2001) such knowledge on nursery habitats spatial distribution may allow managers to better target conservation effort.

5.3.2 *« Atlas des zones de nourriceries de sars (*Diplodus *spp.) et biocénoses marines du Parc National des Calanques » (in prep.)*

The goal of this atlas is to make essential habitat localization available for managers and stakeholders: these data may feed the current discussions following the recent establishment of the National Park and help the process of concertation between stakeholders. Our aim is to provide data that will improve the implementation of the "seascape approach" presented in the previous part; in other words, to adapt the spatial design of management strategies in order to adequately protect essential habitats, allow preserving their functions and permit coastal fish assemblages' replenishment.

The following 10 maps are displayed as a preview of the final version of the atlas. Figure 1 shows the localization of each extract of the atlas along the National Park shoreline.

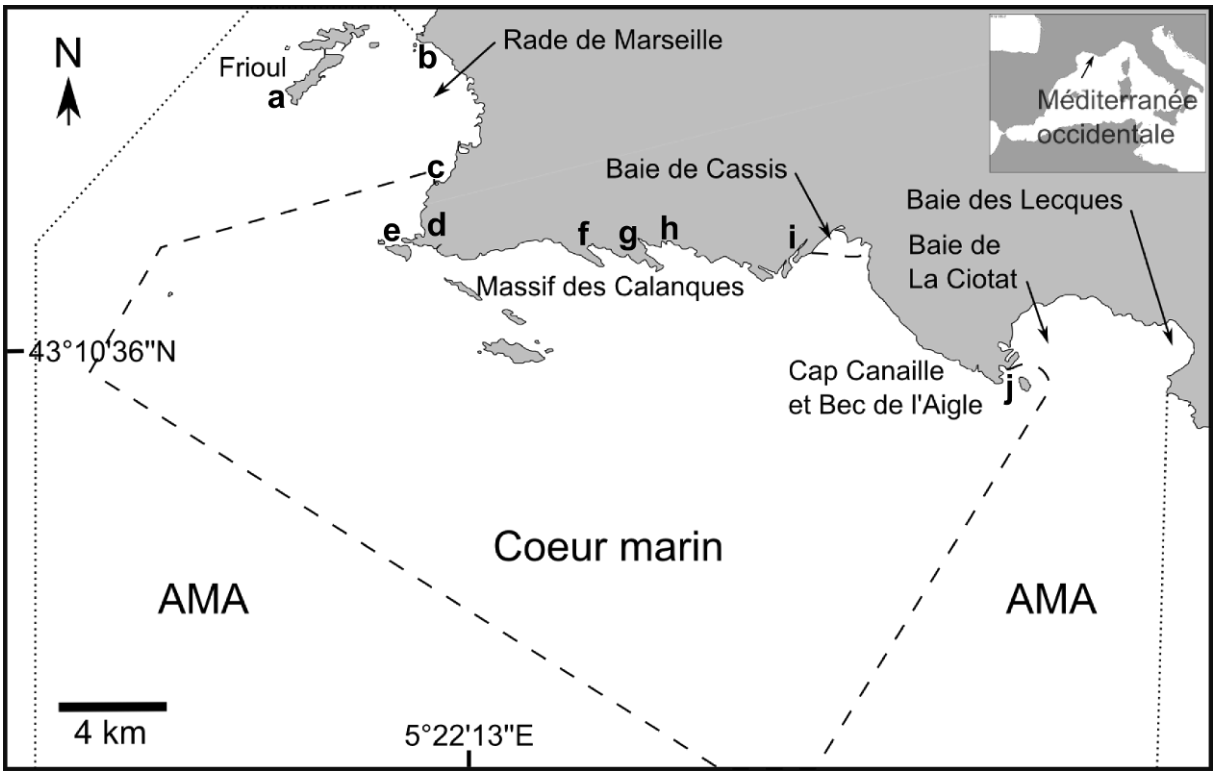


Fig. 1 : "Calanques National Park" shoreline – The localization of the ten extracts from the *Diplodus* spp. nursery habitat atlas (in prep.) are indicated by alphabetic characters (a to j) – Park management plan : Cœur marin (highest protection) ; Aire Maritime Adjacente (AMA = lower protection zone)

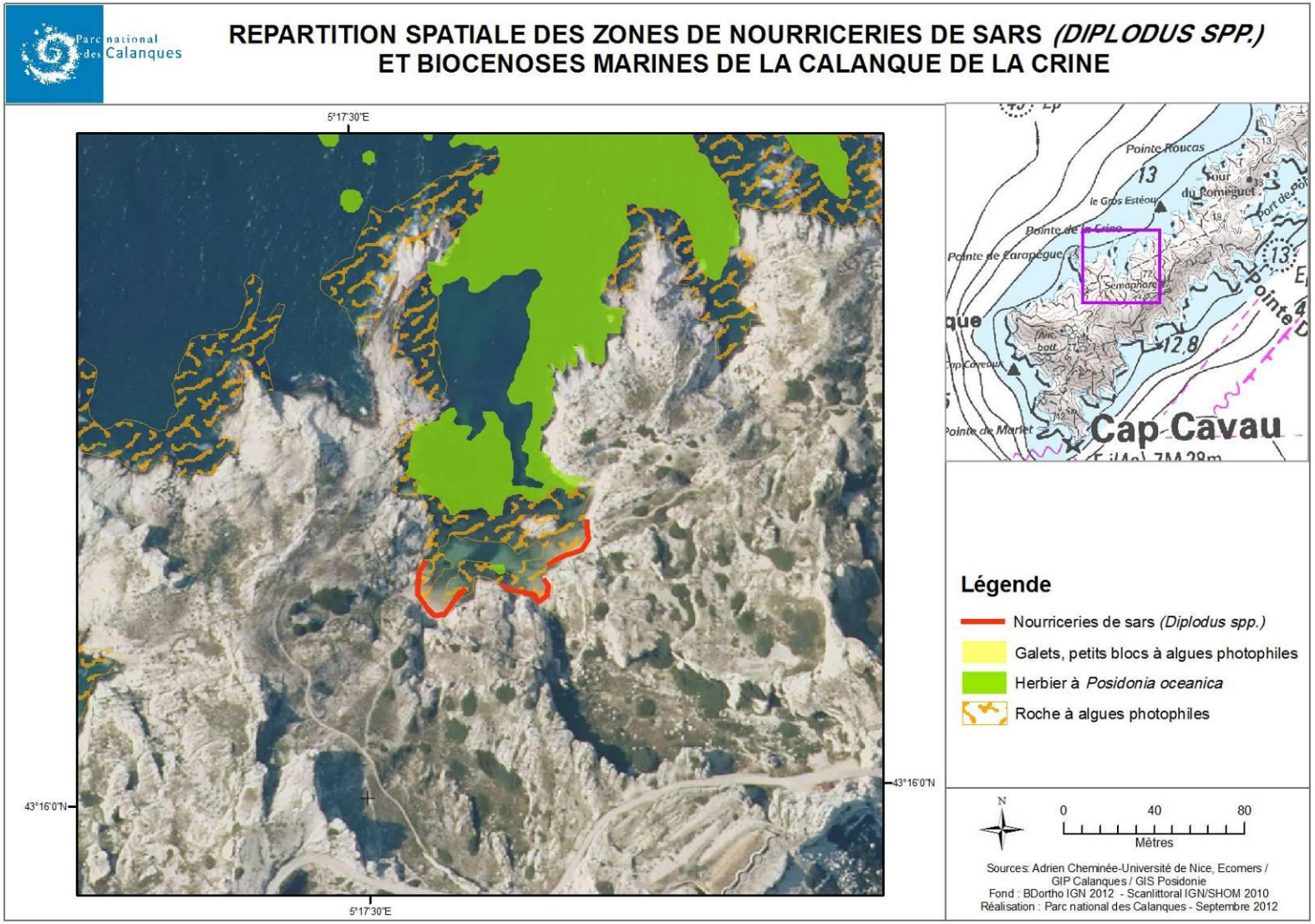


Fig. 1a : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract a (see localization on Fig. 1)

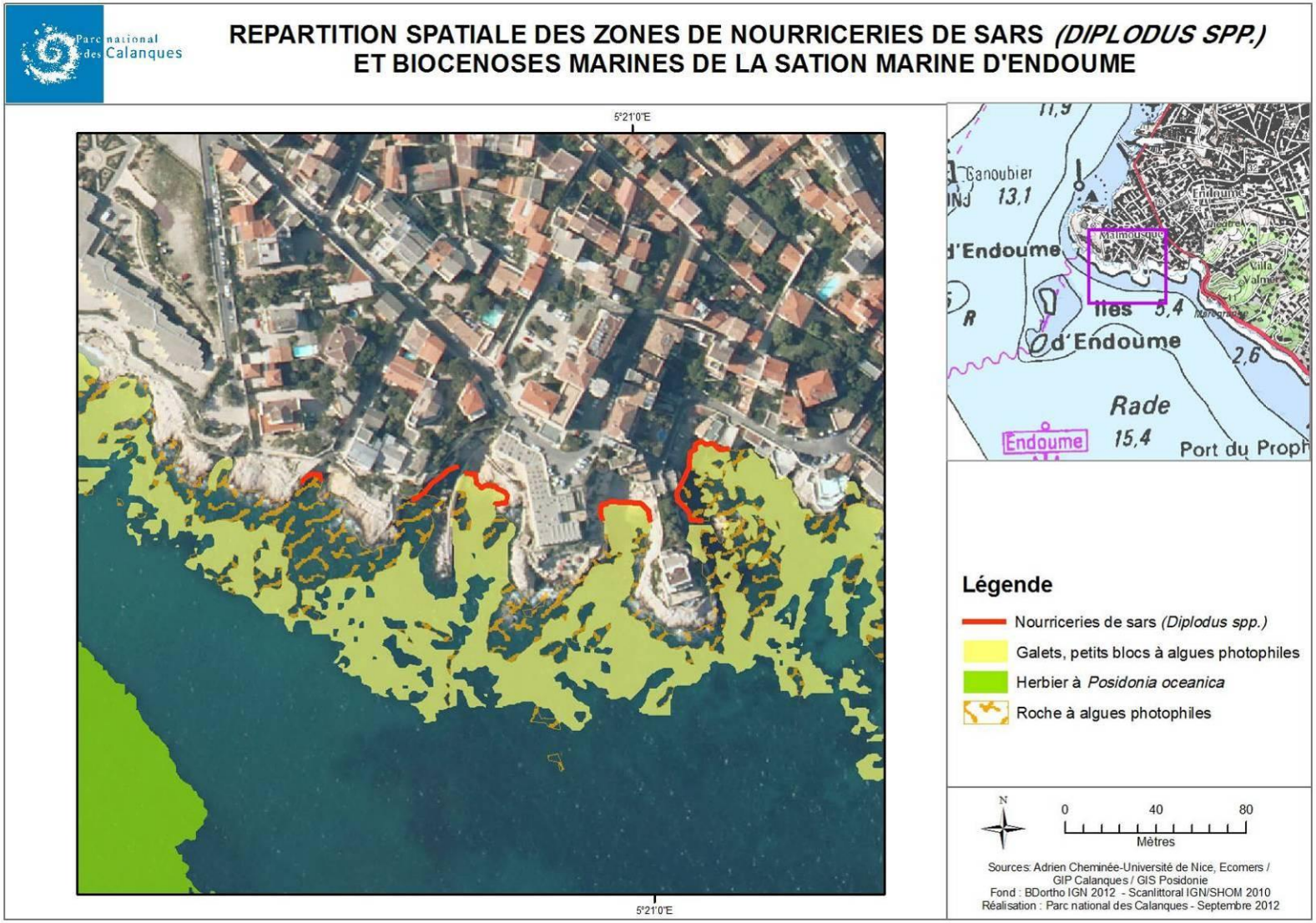


Fig. 1b : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract b (see localization on Fig. 1)

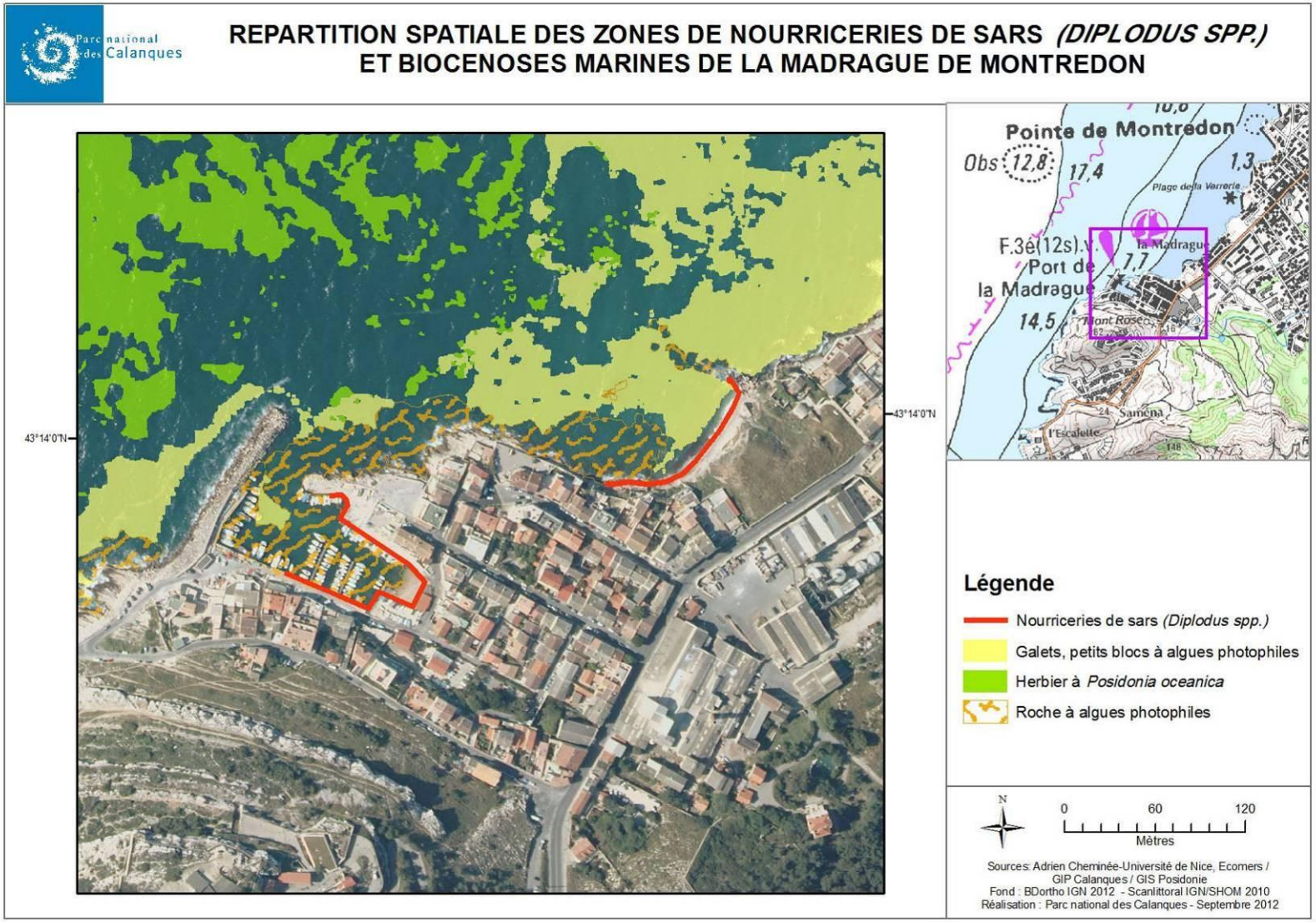


Fig. 1c : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep.)– extract c (see localization on Fig. 1)

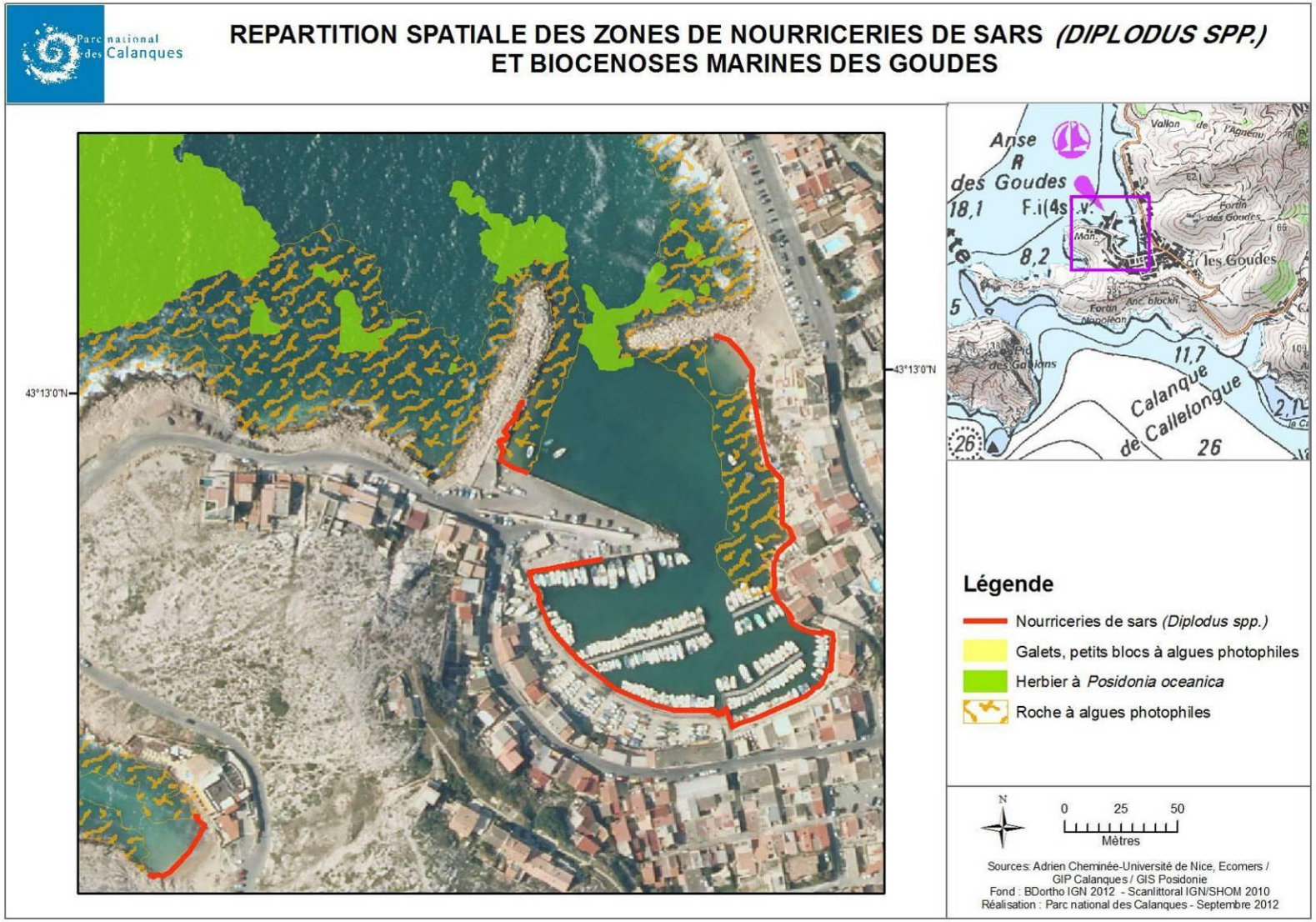


Fig. 1d : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract d (see localization on Fig. 1)

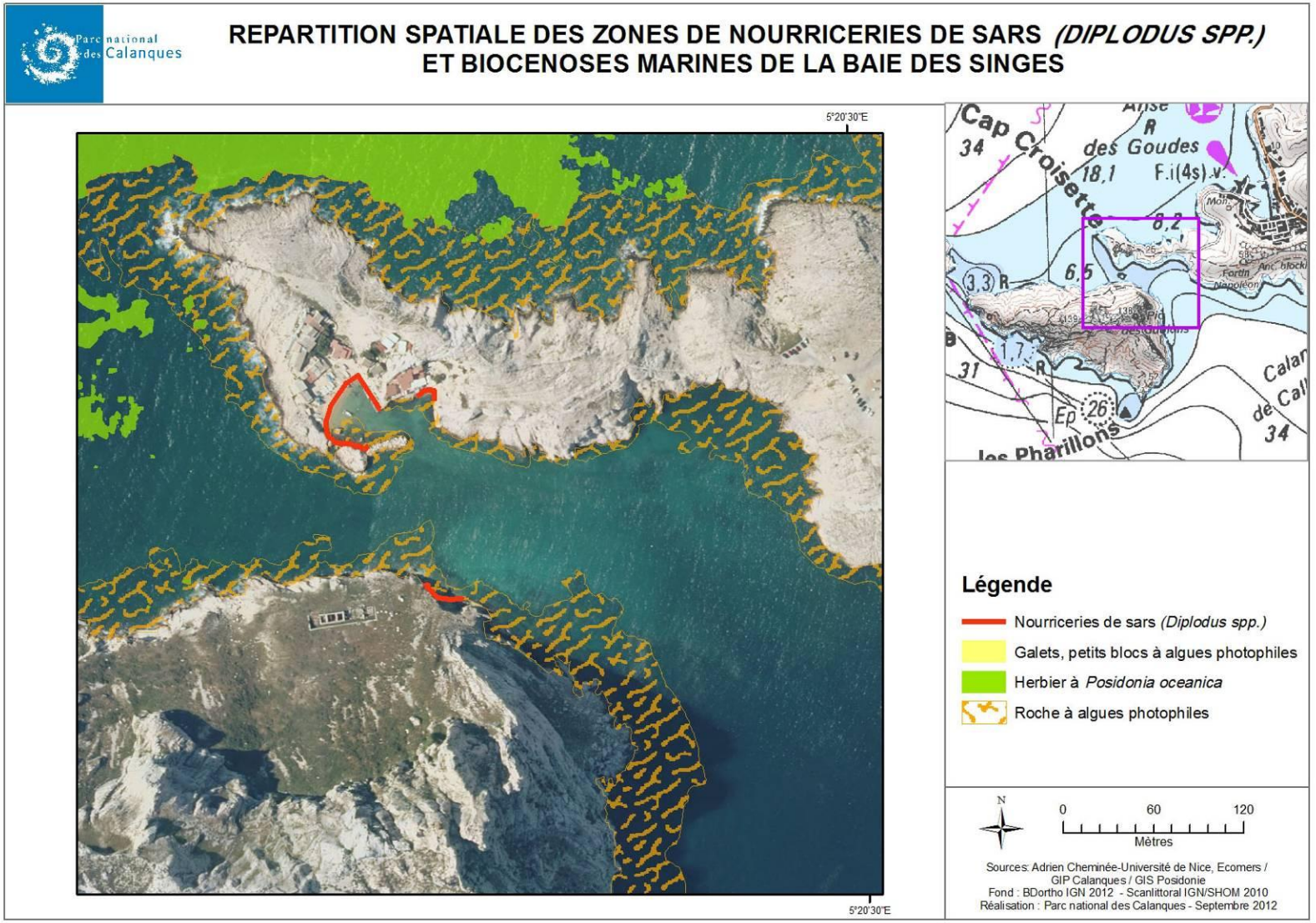


Fig. 1e : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract e (see localization on Fig. 1)

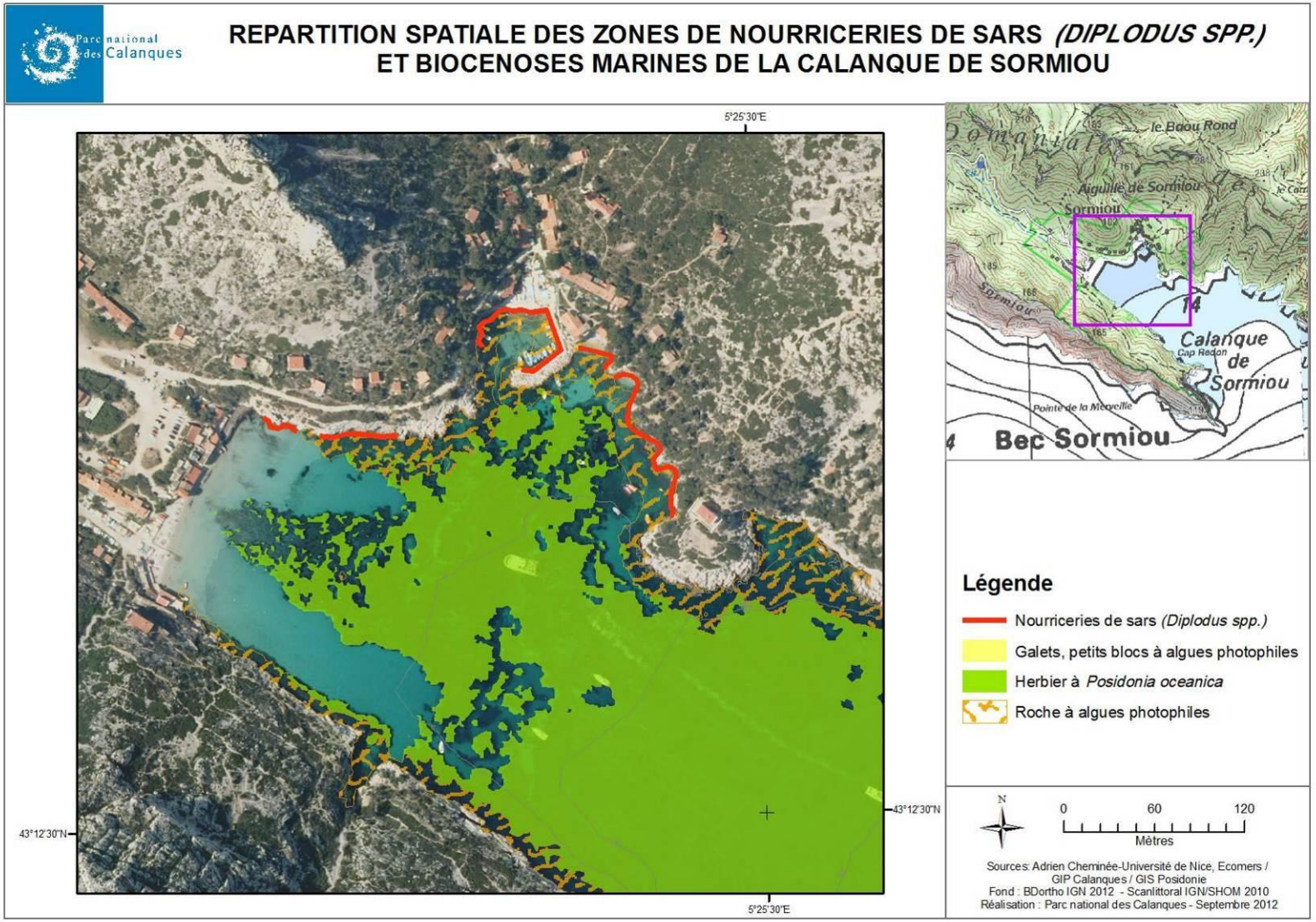


Fig. 1f : Calanques National Park Diplodus spp. nursery habitat atlas (in prep)– extract f (see localization on Fig. 1)

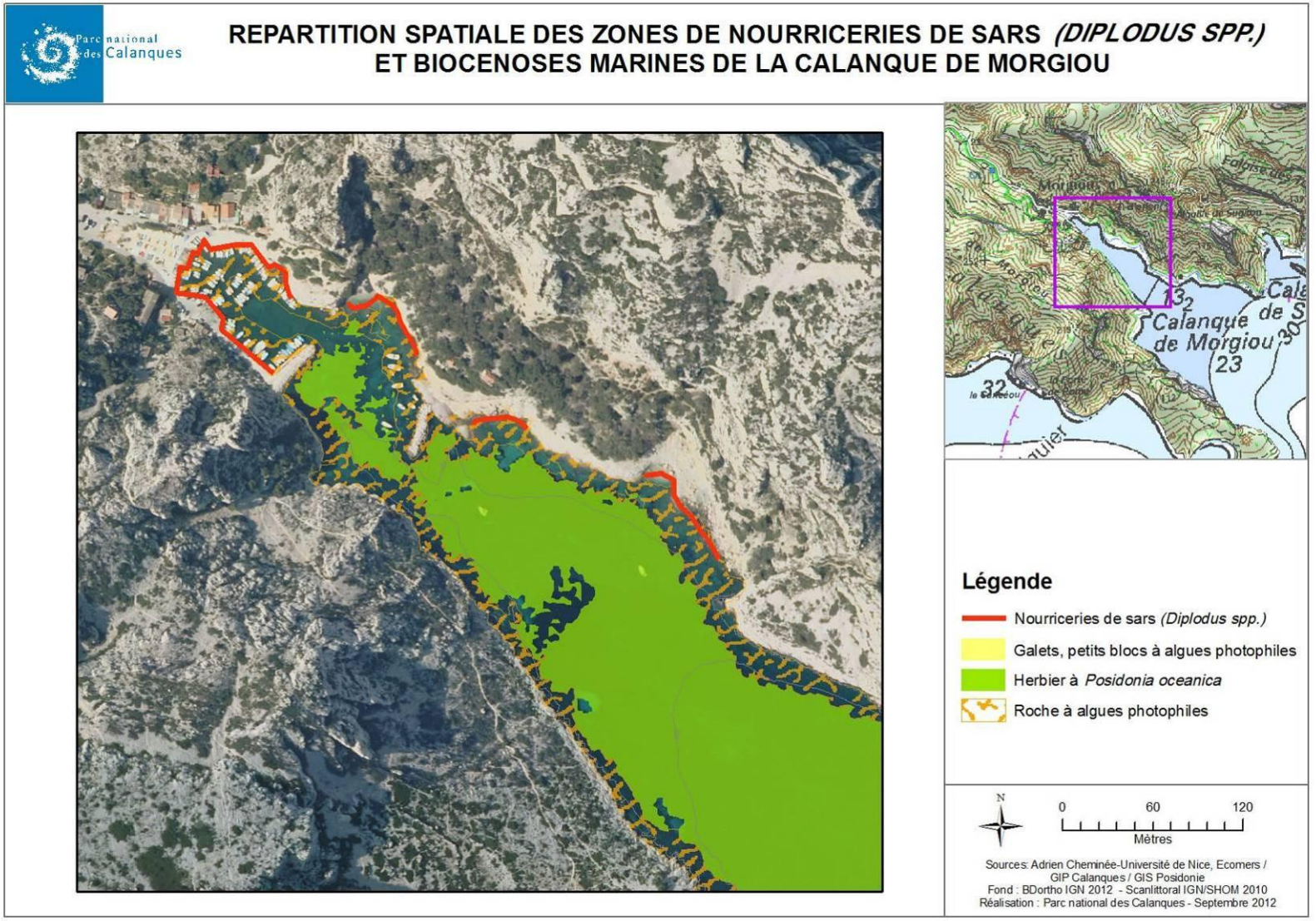


Fig. 1g : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract g (see localization on Fig. 1)

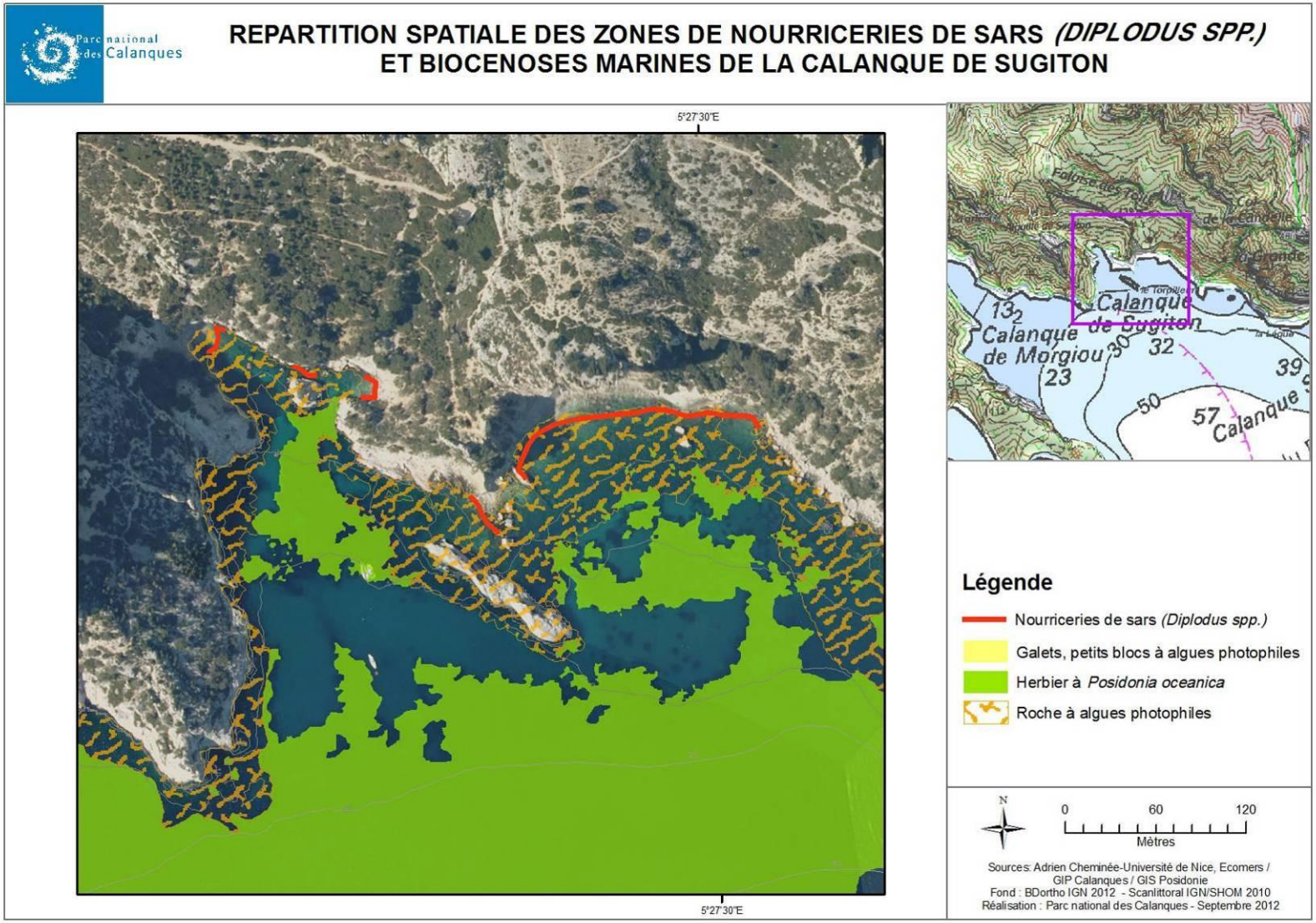


Fig. 1h : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract h (see localization on Fig. 1)

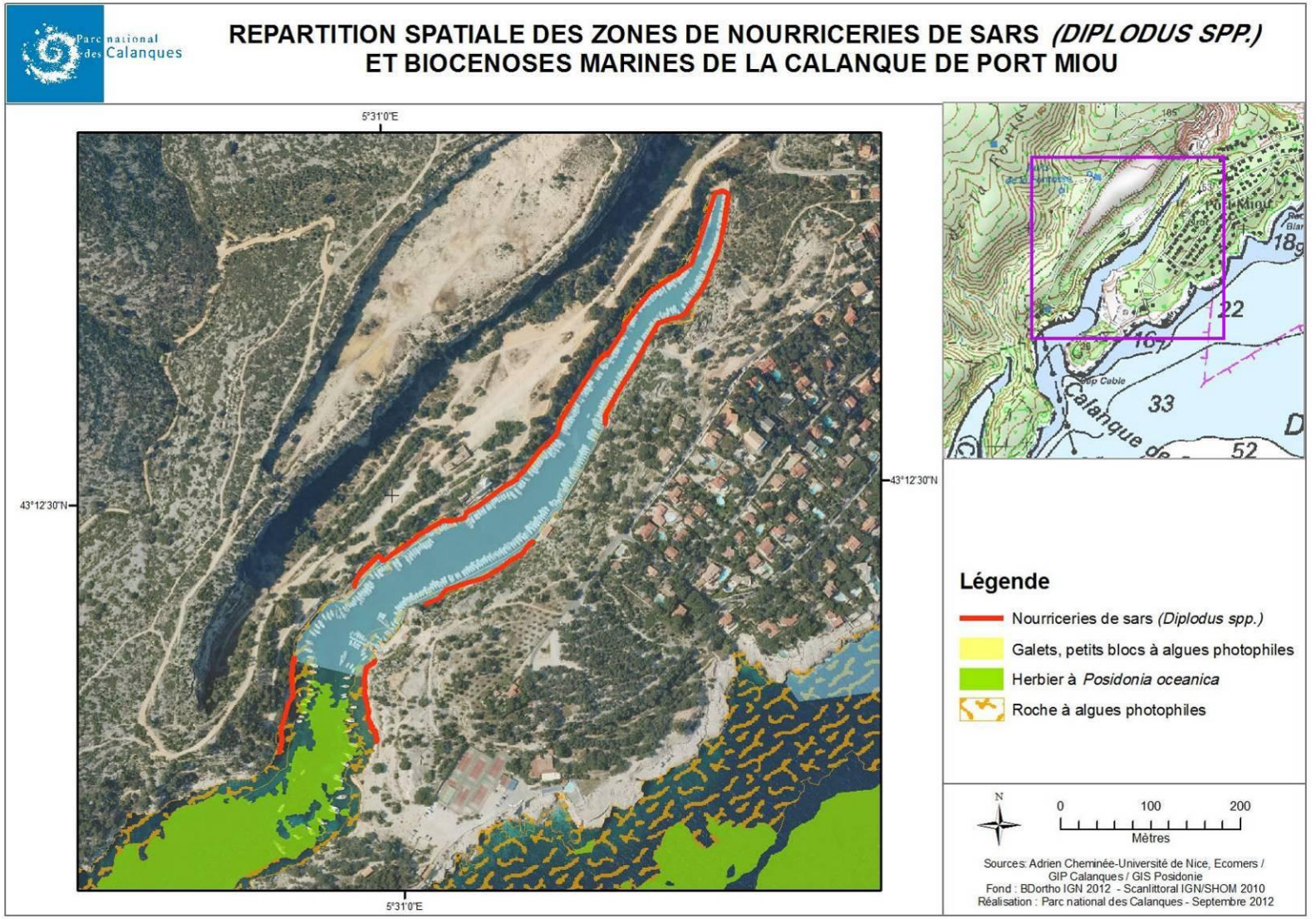


Fig. 1i : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract i (see localization on Fig. 1)

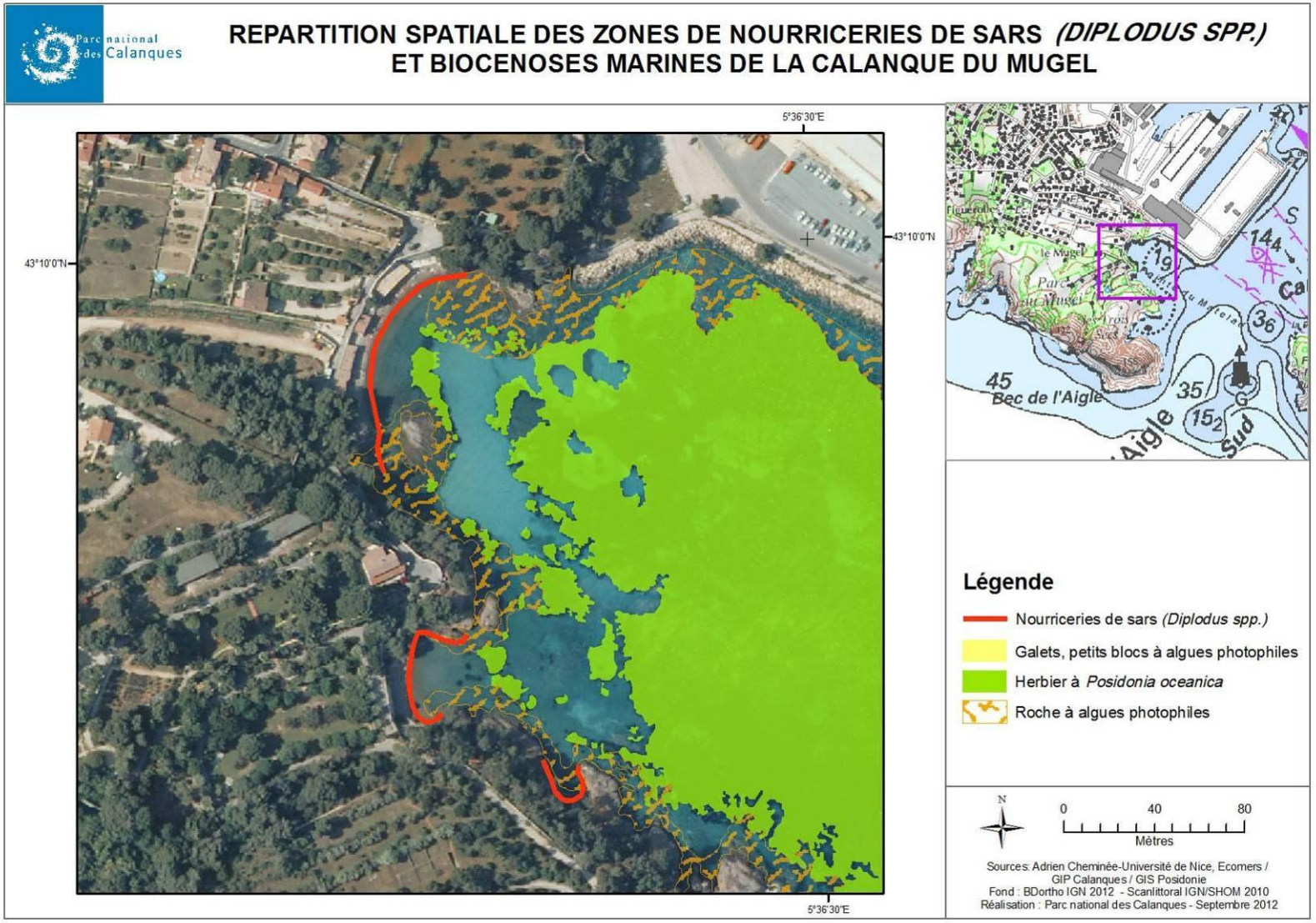


Fig. 1j : Calanques National Park *Diplodus* spp. nursery habitat atlas (in prep)– extract j (see localization on Fig. 1)

5.4 Chapter conclusions

Part 5.2 illustrated how the spatial design of management measures of coastal areas may not fully take the spatial distribution of essential habitats for fish and their connectivity into account. More precisely, current management strategies do take species-focused or in the best case habitat-focused spatial data into account; this is illustrated by the spread of biocenosis cartography works ordered by local administrative bodies (e.g. French DREAL). However these existing processes still neglect the emergent properties of the seascape mosaic that we illustrated in part 5.2. Nevertheless, essential habitat cartography, as illustrated here in the case of the Calanques National Park (part 5.3) can provide managers with the input data necessary to apply a "seascape approach" of coastal management and protection planning.

The localization of essential habitats for a given set of species, along with data on connectivity between them, must be seen as an additional layer of information, to be integrated with other layers describing the state of the coastal areas (human activities, etc.). This may foster the inclusion of a "seascape approach" into the classical steps of management planning of coastal areas: study of the initial state of the environment (natural and human), identification of pressures, threats, and priority issues, definitions of objectives and action plans.

As a perspective (see Chapter VI), such studies should be repeated along Mediterranean coasts in order to 1) localize and quantify essential habitats and 2) assess which proportion of them is really protected. In the case of *Diplodus* spp. for example, while such data are partly available for the northern part of the Mediterranean (France, Spain, Italy), data are mostly lacking along the southern coast of the basin where detailed field investigations are still required.

Chapter VI. General discussion and perspectives

Cabra Salada, Fornells Bay, Menorca, Balearic Island, 12th July 2011. Exploration of shallow micro-habitats in order to select new study sites: that we developed a collaborative study between my lab (Ecomers) and the Marine Station “Jaume Ferrer”-IEO) aims at comparing the nursery value of various macrophyte-formed habitats.

Chapter VI. General discussion and perspectives

6.1 The initial questions…

The main question that prompted this PhD was to better understand the characteristics and consequences of the transformation of Mediterranean infralittoral fish nursery habitats in order to gather useful knowledge for managers of coastal areas. More precisely, my main objectives were: (1) to assess the relative nursery value of various macrophyte-formed habitats displaying different tri-dimensional structure, notably *Cystoseira* forests and Dictyotales-Sphacelariales bushland, among others habitats of the Infralittoral seascape mosaic; (2) to investigate their spatial distribution along rocky shores (localization and quantification); (3) to find out whether settlers densities in nursery habitats are consistent through space and time; (4) to identify the consequences of habitat transformations with respect to their function for juvenile fishes. Answering these questions (1 to 4) also led me to focus on the underlying processes shaping juvenile abundance patterns across habitats. Ultimately (5) I estimated if and how could essential habitats and their connectivity (nursery habitats and other adult habitats) be taken into account by coastal management measure design.

6.2 Main results

The conclusions in each chapter provide specific answers at each of these questions. The aim of this final Chapter is to look beyond the data in order to obtain a broader vision of nurseries and other essential habitats at the scale of Mediterranean seascapes. Indeed, as a final conclusion, the results I gathered during this PhD and related collaborations highlighted that both the study and the management of fish essential habitats and assemblages must consider nested spatial scale of analysis and adopt a "seascape approach":

1) Through my work I highlighted the high nursery value –*sensu* Beck et al. (2001)- of two infralittoral rocky habitats: the *Cystoseira* forests and the shallow heterogeneous bottoms of blocks and pebbles. Both habitats displayed on average higher densities of fish juveniles (mainly labrids and sparids species, respectively) than other surrounding rocky habitats. The high nursery value of these habitats was consistent through time (between years) and space (at local and regional scales): in every NW Corsican site studied, *Cystoseira* forests displayed on average higher densities of notably *Symphodus* spp. juveniles than others adjacent rocky habitats such as the Dictyotales-Sphacerlariales bushland (Chapter III). In various sites along Marseilles and French Riviera rocky coasts (Chapters II part 2 and 3) we confirmed the high nursery value of shallow blocks and pebbles bottoms for *Diplodus* spp. juveniles demonstrated by previous studies (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien et al., 1995; MacPherson, 1998).

2) However, these essential habitats were not homogeneously distributed along the coasts and their spatial distribution covered a low proportion of the rocky shorelines. The nursery habitats (shallow heterogeneous blocks and pebbles) of *Diplodus* were scarce (less than 10% of shorelines) for both localities studied (Chapter II). In the case of *Cystoseira* forests, I did not precisely assess the availability of this habitat along rocky shores, but previous works highlighted their scarcity following their dramatic decline in many localities from the North-western (Thibaut et al., 2005) and Eastern Mediterranean (Sala et al., 2011).

3) Furthermore, the present work highlighted that settlement intensity (density of settlers) in these nursery habitats was highly variable in space, both at local (<1 km) and regional (20 km) scales for *Diplodus* spp. (Chapter II) and *Symphodus* spp. (Chapter III-part 3). This was consistent with previous studies in other macrophyte- formed habitats (Thistle *et al.*, 2010) or for *Diplodus* spp. juveniles for which Vigliola et al. (1998) showed a strong inter-annual and spatial variability of juvenile densities in nurseries at 20 sites dispersed along the NW Mediterranean basin rocky shores. Such spatial variability may be partially explained by oceanographic patterns that shape larval dispersal, settler input in nurseries and consecutive juvenile density patterns in space (Di Franco and Guidetti, 2011).

4) Subsequently, at a local scale, residual variability in juvenile densities within a given nursery habitat (as seen in *Cystoseira* forests in Chapter III-part 3) or density patterns across habitats (Chapter IV) may be explained by different tri-dimensional structures of different habitats (or degraded facies of a given habitat). These determine their quality for juveniles, *sensu* Hindell et al. (2000), i.e. mainly the ratio food availability/predation rate, resulting in active choice and or differential mortality of juveniles between habitats (Thiriet et al., accepted) as explained in Chapter III-part 5. The various chapters of this thesis illustrated at each spatial scale how habitat transformations may induce changes of tri-dimensional structure –*sensu* August (1983)– of seascapes and consequently alter their nursery value for fishes. Indeed, based on August (1983) seascape tri-dimensional structure may be define as the addition of various spatially nested components: (a) at the scale of seascape (about 2 km), the seascape "heterogeneity" is determined by i) its composition (number of distinct units) and ii) their ordination (degree of fragmentation and relative positions); (b) within a given unit of the seascape (for instance one habitat such as a *Cystoseira* forest), the tri-dimensional structure is defined by its "heterogeneity" again (subdivision in micro-habitats) and its "complexity" (for instance the tri-dimensional architectural arrangement, such as the degree of ramification of the arborescent strata). Given these definitions, the previous chapters showed how this tri-dimensional structure of seascapes, and its transformation through anthropogenic impacts in particular, acted at nested spatial scales within the Infralittoral and shaped juvenile fish abundances patterns. In this respect, the most relevant observations were:

   - At the scale of habitats (a) the homogenization of shallow heterogeneous bottoms of blocks and boulders by addition of homogenous mono-grain-sized sediment during beach profiling reduced their nursery value for *Diplodus* spp. juveniles (Chapter II-part 2); (b) arborescent "complex" macrophyte-formed habitats (*Cystoseira balearica* and *C. crinita* forests) hosted 9 to 12 fold more *Symphodus* spp. juveniles than less complex Dictyotales-Sphacelariales (DS) bushland (Chapter III-parts 2 and 3, Chapter IV-part 2). (c) During e*x-situ* experiments (Chapter III-part 5) we observed active micro-habitat choice for juveniles of *Symphodus* spp., which was modulated by the type of predator present, and differential predation success of *Serranus* spp. according to the habitat complexity (arborescent forest *vs.* bushland): more complex habitat, offering more refuges lowered predation success.

   - At an intermediate spatial scale between a single habitat and the seascape mosaic: (d) alteration of a *Cystoseira* forest, which was simulated by i) reduced canopy density (lowered complexity) and ii) canopy fragmentation and patch-size reduction (increased heterogeneity), dramatically reduced its nursery value for *Symphodus* spp. juveniles, which was three times lower in a fragmented forest, Chapter IV-part 2). At the same time, this fragmentation increased heterogeneity (i.e. by interspersing two

habitats: patchy *Cystoseira* + patchy DS) and consequently was favorable to *Coris julis* juveniles through edge effects (Chapter IV-part 2): the nursery value of the same area was consequently increased for this taxa at this scale.

- At the scale of the seascape mosaic (e) the complementarity of various coexisting nursery habitats (heterogeneity) for various juvenile taxa may satisfy a greater number of species than a single homogenous habitat covering the equivalent area. This is predictable according to the concept of spatial partition of juveniles of various species within various habitats, described for Sparidae in a previous study (Harmelin-Vivien et al., 1995). In contrast (f) seascape homogenization due to *Caulerpa taxifolia* invasion was detrimental to *C. julis* recruitment (Chapter IV-part 3).

5) Furthermore in order to complete the fish species life cycle and population replenishment, nursery habitats and other essential habitats of the life cycle, such as adult spawning grounds, must be abundant enough and connected at various nested spatial scales (Di Franco et al., 2012). In my study case (Chapter V-part 2), the current design of management measures did not take into account sufficient amounts of essential habitats and the connectivity between them at each life stage (larvae, recruits, adults). We proposed a conceptual scheme aiming at adopting such "seascape approach", in order to guarantee coastal fish assemblages' replenishment (Chapter V).

In conclusion, the examples provided throughout all the previous chapters converge to make us state that the analysis of processes shaping the ecological functions (in particular the nursery role) of infralittoral habitats, as well as the design of management measures aiming at preserving the function of coastal areas, must consider various nested spatial and temporal scales.

6.3 Further discussion and identification of perspectives for research and management

In the frame of this PhD I developed collaborative works with other researchers in order to study abundance patterns of juvenile fishes across habitats in Mediterranean seascapes. I present here some of our scientific objectives as part of perspectives of my work: a joint effort of Mediterranean marine ecologist may allow us to explore the numerous remaining scientific questions and provide managers with useful data.

Theories and experiments about underlying processes explaining juvenile abundance patterns have been previously developed and performed in other temperate and tropical seas (Horinouchi *et al.*, 2009b; Horinouchi and Sano, 1999; Nanjo *et al.*, 2011) but Mediterranean examples remain scarce (Thiriet et al., accepted). Quantifying food availability and estimating predation rates, i.e. more globally trophic network of the *Cystoseira* forests and alternate stable states –*sensu* Knowlton (2004)– requires deeper

studies in order to fully understand processes shaping abundance patterns of juveniles across habitats and to better predict habitat transformation consequences. The results obtained in my PhD will serve as a base for P. Thiriet's PhD thesis (in prep.), which explores these aspects, at various spatial scales within the NW Mediterranean in sites nested in localities of Corsica, Menorca (Balearic Island) and the French Riviera. This work will notably help testing hypothesis built on my work in Chapter IV, namely food availability and accessibility for juveniles, trophic chains and predation rates. Ultimately, in areas where *Cystoseira* forests have already disappeared, the exact quantification of how much productivity is virtually lost because of the absence of the forests is a priority task for future researches.

Previous studies highlighted the high nursery value of *Posidonia oceanica* meadows for some taxa (e.g. *Spondyliosoma cantharus*, *Diplodus annularis*) (Francour and Le Direac'h, 1994; Francour and Le Direac'h, 2001) particularly in comparison with sandy bottoms or rocky DS bushland (Guidetti, 2000; Guidetti and Bussotti, 1997). In the present research (Chapter III-part 4) I gathered some preliminary data aiming at comparing *Cystoseira* forest *vs. Posidonia oceanica* meadows juvenile densities. These comparisons between different macrophyte-formed habitats nursery value are crucial to better understand the complementarities of habitats of the seascape mosaic for juveniles. Thus, based on the results presented here further studies with an adapted methodology for this last habitat and a larger sampling effort are being performed in the bay of Fornells (Menorca) to compare juvenile densities of various macrophyte-formed habitats (*Cymodocea nodosa*, *Cystoseira barbata*, *Caulerpa prolifera*, Fig. 2). This is done in a collaborative study we developed in the frame of A. Cuadros-Casado PhD thesis (in prep). Furthermore, among *Cystoseira* forests, at the scale of the seascape, I highlighted that although *Cystoseira* forests' higher nursery value (*versus* DS bush) was consistent through space, juvenile densities at a given depth (about 4-5 meter) displayed strong spatial variability (Chapter III). However, although the vertical density distribution of juveniles has been previously studied in others rocky habitats (Garcia-Rubies and Macpherson, 1995; Letourneur et al., 2003), no studies have investigated up to date the influence of depth on *Cystoseira* forest nursery value. During my study of spatial (horizontal) variability of juvenile densities in *Cystoseira* forests (Chapter III-part 3) I showed that spatial variability of *Symphodus* spp. juvenile density was partly correlated to habitat three-dimensional structure (canopy height, %cover) and also partly related to abiotic factors such as small variations of depth. Letourneur et al. (2003) also found that labrid juvenile densities were correlated to depth, displaying the highest densities in the first 10 meters. Spatial differences on juvenile densities (Tupper and Juanes, 1999) or on juvenile mortality rates (Arceo et al., 2012) have been previously explained by adult conspecific and predators density spatial distribution. Similarly, depth distribution of juveniles, for a given habitat, may also be shaped by the spatial distribution of adult conspecific and predator densities, which in turn are influenced namely by protection levels (Polunin and Roberts, 1993). The results

obtained in Chapter III-part 3 are therefore used as a base for another collaborative study (Cuadros-Casado et al., in prep) to analyze juvenile density patterns within *Cystoseira* forests according to both depth (0-15 meters) and protection levels (no-take area *versus* non-protected) around Menorca Island.

As a first conclusion, better knowledge of the relative nursery value of all infralittoral habitats of a given locality is necessary to perform the best management choices. Furthermore, this knowledge must be completed by the understanding of parameters responsible of site-specific variation in the nursery value of a given habitat: once these data may be gathered, managers may be able to know which proportion of the Infralittoral is vital for fish recruitment and will be able to target properly essential habitats conservation efforts (Beck et al., 2001). The understanding of site-specific variations in the nursery value of a given habitat may be performed through multivariate analysis of the effect of biotic and abiotic factors (Beck et al., 2001) including e.g. tri-dimensional structure, food availability, depth, etc. Our article in preparation[19] will adopt such approach. Ultimately, for *Cystoseira* forests as well as for each other habitats, we may be able to describe the set of biotic and abiotic parameters which favor the best habitat nursery value for juvenile fishes.

Finally, the data gathered in this thesis about juvenile density patterns in *Cystoseira* forests and predation can be used as a base for the study of the other factors that contribute to this habitat nursery value (Beck et al., 2001): namely success of recruits movements towards other, adult habitats. For *Diplodus* spp., at a wide spatial scale (e.g. French Riviera), Chapters II and V highlighted that connectivity between every essential habitat (reproduction habitats, nursery habitats) must be assessed for each life-cycle stage (larvae, recruits, adults) in order to better understand replenishment and to better design management measures for fish assemblages and habitats. Although some studies have been performed in this respect along the Adriatic coast (Di Franco et al. (2012), specific assessments are needed at each locality to cope with local particularities. In the frame of such perspective, current works are ongoing, such as those lead in the frame of MMMPA Training network (J.A. Garcia-Charton and collaborators) or in the frame of A. Cuadros Casado PhD thesis which studies the impact of oceanographic circulation patterns around Menorca Island on *Diplodus* spp. settlement patterns. Another project developed in the Villefranche Oceanographic Observatory (J.O. Irisson and collaborators) involves the study of larvae behavior in the pelagic water column (orientation and active swimming) with methodologies already used in tropical waters (Irisson, 2008; Irisson et al., 2009). The connectivity between juvenile and adult habitats is a key component of habitat nursery value : Beck et al. (2001) highlighted that even if a habitat displays high densities of juveniles, if these are not able to reach adult habitats, then the nursery value of this juvenile habitat is reduced and it does not play a nursery role. This is why connectivity is a key process of seascapes (Cowen et al., 2007; Cowen and Sponaugle,

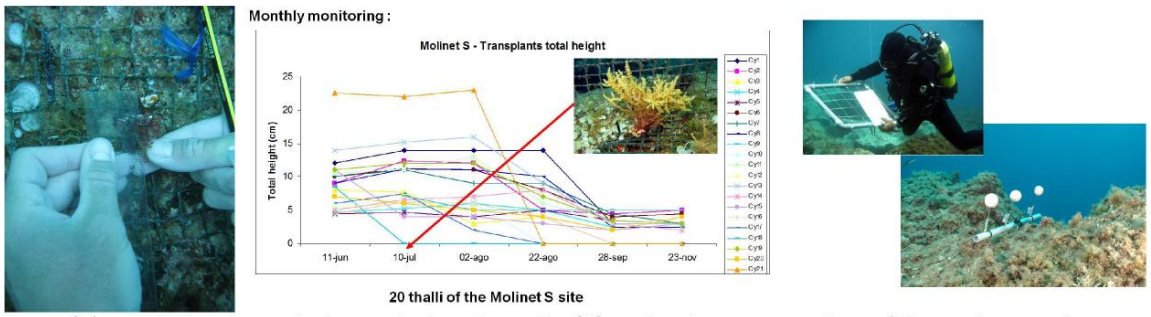
[19] See Chapter III-part 3

2009; Gillanders et al., 2003; Mumby, 2006); seascapes are not only a juxtaposition of habitats: energy and biomass exchanges through connectivity give them emerging properties.

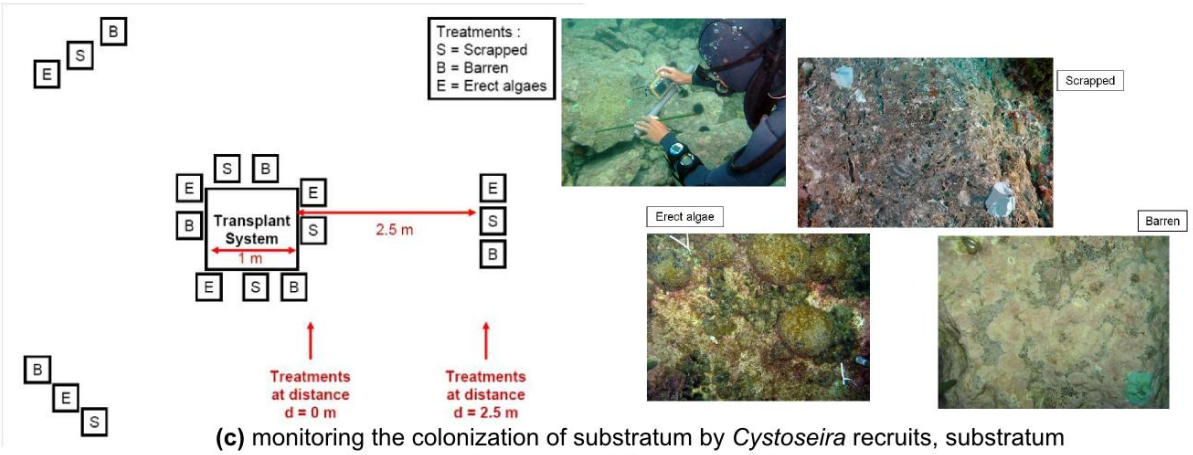
In coastal areas where *Cystoseira* forests have totally disappeared, the results of my PhD thesis support the idea that restoration of the forests (Sales et al., 2011; Susini et al., 2007) may be an ultimate tool to renovate the biodiversity of coastal areas and more particularly the productivity of coastal fish assemblages. Indeed, I highlighted that abundant juvenile fishes may rely on the tri-dimensional structure offered by the forest to take refuge. If the initial causes of the forest regression have been solved, restoration of the canopy-forming complex forest in areas currently dominated by low-complexity Dictyotales-Sphacelariales assemblages, could enhance survival of fish juveniles and consequently the production of recruits to adult assemblages. I performed in 2008 a pre-doctoral research project in the frame of a project led by E. Sala around the Medes Island (Catalunya, Spain). This project (Cheminée, Hereu, Sala et al.; unpublished data) aimed at (1) testing a transplantation technique for *Cystoseira elegans* and (2) monitoring the development of restored forests and associated community (notably fish juveniles). More particularly it consisted (Fig. 1) in (a) transplanting fertile *Cystoseira* individuals along the coast of Montgri where forests have disappeared; (b) monitoring transplants survival and growth; (c) monitoring the colonization of surrounding substratum by *Cystoseira* recruits in order to study substratum preferences and dispersion distances; (d) monitoring various parameters of the environment (e.g. fishes and sea-urchins densities, temperature, hydrodynamism, water quality, etc.). The experiment started in April 2008, 8 months later preliminary results were promising: some first *Cystoseira* recruits where observed around the transplants (Fig. 1e). Unfortunately, December 26th 2008, a centennial storm ravaged the entire coast of Catalunya, deeply transformed the coastal habitats (Garcia-Rubies et al., 2009; Navarro et al., 2011) and totally destroyed the experiment, before final results could be gathered.

Two years later, a collaboration was developed with a team of the Spanish Oceanographic Institut (IEO) based in the Balearic Islands (Menorca), where M. Sales, K. Ballesteros and collaborators had previously developed transplantation methods for *Cystoseira barbata* (Sales et al., 2011). Our ongoing collaborative project started in summer 2011. It aims at monitoring if the restored new *Cystoseira* forests get colonized by juvenile of fishes, as in natural forests, i.e. if restored forests recover a high nursery value for fishes. Field monitoring was initiated using the methodology described in my thesis (Fig. 2), as for the other collaborative studies mentioned earlier.

(a) transplanting fertile *Cystoseira* individuals along the coast of Montgri where forests have disappeared



(b) monitoring transplants survival and growth; **(d)** and various parameters of the environment



(c) monitoring the colonization of substratum by *Cystoseira* recruits, substratum preferences and dispersion distances

(e) *Cystoseira* recruits observed in monitoring quadrates

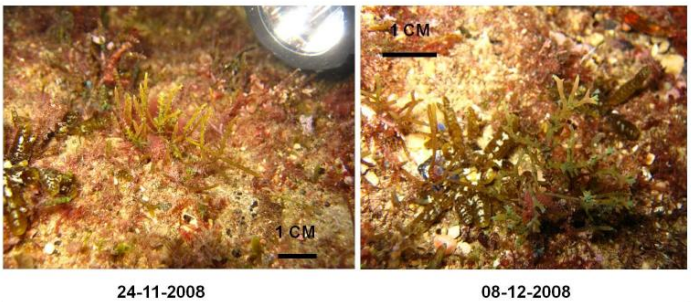


Fig. 1: development of a transplantation protocol for *Cystoseira elegans* (Medes Island, Montgri coast, Catalunya, Spain, April to December 2008) (Cheminée , Hereu, Sala et al., unpublished data)

Fig. 2 : collaborative field work at Menorca islands - *in situ* training to assess juvenile densities in various macrophytes-formed habitats, including natural *C. barbata* forests, *Caulerpa prolifera* and *Cymodocea* sp. meadows (right picture) and restored *Cystoseira* forests (Menorca, Balearic Islands, July 2011)

6.4 Final conclusion

In the Mediterranean, current management measure designs do not take into account the spatial distribution of essential infralittoral habitats and their connectivity (Chapter V). In other regions, especially along tropical coasts, data on essential habitats of marine species are being used to shape coastal developments and protection programs (Cheminée, 2002; Gabrié et al., 2007). As a conclusion, in the Mediterranean, for each locality of interest, for each considered fish species, this PhD thesis and future works gathering knowledge on essential habitats identification, localization, quantification and connectivity will provide managers with essential data to establish a multi-taxa seascape approach for the design of management measures, encompassing various nested spatial scale and integrating several taxa specificities: nowadays, after decades of local-scale, mono-taxa-focused (or in the better case single-habitat-focused) legislative and technical practices, coastal management must upgrade to the wider seascape mosaic scale. Chapter V proposed a conceptual framework to apply such approach: however it must be acknowledged that each locality, according to its particularities, will always require its own case by case study.

6.5 Conclusion finale (French translation)

En Méditerranée, le design actuel des mesures de gestion côtière ne prend pas en compte la distribution spatiale des habitats essentiels de l'Infralittoral, ni leur connectivité (Chapitre V). Dans d'autres régions, notamment dans les mers tropicales, les données concernant les habitats essentiels aux étapes clefs du cycle de vie des organismes marins sont utilisées pour moduler les programmes de développement et optimiser ceux de protection des zones côtières (Cheminée, 2002; Gabrié et al., 2007). En conclusion, en Méditerranée, pour chaque localité, pour chaque espèce de poisson considérée, cette thèse de doctorat, associée aux futurs travaux procurant des connaissances sur l'identification, la localisation, la quantification des habitats essentiels et leur connectivité, peux fournir aux gestionnaires les données nécessaires pour adopter une approche multi-spécifique, à l'échelle des paysages sous-marins, pour le design des mesures de gestion ; c'est-à-dire prenant en compte plusieurs échelles spatiales imbriquées et intégrant les spécificités d'espèces variées. De nos jours, après des décennies de pratiques techniques et réglementaires restreintes à une échelle locale, mono-spécifique (ou au mieux mono-habitat), la gestion des zones côtières doit adopter une approche située à l'échelle globale des paysages. Le Chapitre V propose un schéma conceptuel permettant d'appliquer cette approche : cependant ceci ne doit pas faire perdre de vue que chaque localité, avec ses particularités, nécessite une étude détaillée, au cas par cas.

Chapter VII. Appendix - valorization of the PhD works

Pedagogic exploration of shallow habitats from the cove “Calanque de la Crine”, Frioul archipelago, Marseilles, France (5th of August, 2011) ; these excursions, open to the general public, are co-organized by two NGOs: “Septentrion Environnement” a scientific NGO from which I am a member, and “Boud’mer”, a cultural NGO, both based at Marseilles – During my PhD I led various vulgarization and academic lectures and field courses based on knowledge acquired trough this thesis. Photography by O. Bianchimani.

Chapter VII. Appendix- valorization of the PhD works

7.1 List of papers (published or in prep.)

- **Chapter II**

CHEMINEE, A., FRANCOUR, P., and HARMELIN-VIVIEN, M. (**2011**). Assessment of *Diplodus* spp. (Sparidae) nursery grounds along Marseilles rocky shores (France, NW Mediterranean) (Published in Scientia Marina 75(1), 181-188.)

ARCEO H., CHEMINÉE A., BODILIS P., MANGIALAJO L. and FRANCOUR P. (**2012**). Fishery reserve effects on sparid recruitment along French Mediterranean coasts (Published in the Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012 - 13E Fisheries: General session)

- **Chapter III**

CHEMINEE A., SALA E., PASTOR J., BODILIS P., THIRIET P., MANGIALAJO L., COTTALORDA J.-M. and FRANCOUR P. (**under review**). Nursery value of *Cystoseira* forests and the replenishment of Mediterranean rocky reef fishes (submitted to JEMBE).

CHEMINEE A., PASTOR J., THIRIET P., BIANCHIMANI O., COTTALORDA J.-M. and FRANCOUR P. (**in prep**). Spatial and temporal variability of fish juvenile densities within *Cystoseira* forests.

THIRIET P., CHEMINEE A. and FRANCOUR P. (**accepted**). Nursery role of macrophytes-formed habitats: abundance patterns and underlying processes under a seascape approach. In «Sub-marine seascapes», Agence des Aires Marines Protégées. Ed. Springer.

THIRIET P., CHEMINEE A., FRANCOUR P. et al. (**in prep**). Differential habitat use, anti-predator behavior and mortality of juvenile *Symphodus* spp. (Pisces : Labridae) in response to multiple functional types of fish predators.

- **Chapter IV**

CHEMINEE A., SALA E., PASTOR J., THIRIET P., BIANCHIMANI O., ARCEO H., CLOZZA M., CUADROS-CASADO A., MARTIN-LESCANNE J., COTTALORDA J.-M. and FRANCOUR P. (**in prep**). Consequences of patch-density decrease, patch-size reduction and fragmentation of *Cystoseira* forests on their nursery value for Mediterranean juvenile fishes.

CHEMINEE A., MERIGOT B., VANDERKLIFT M.A., MEIER P. and FRANCOUR P. (**in prep**). Does loss of habitat complexity alter fish recruitment? Preliminary results from the Mediterranean example of *Caulerpa taxifolia* invasion (submission to Biological invasions).

- **Chapter V**

CHEMINEE A., FEUNTEUN E., CLERICI S., COUSIN B. and FRANCOUR P. (**accepted**). Gestion des habitats de l'Infralittoral : adopter une approche à l'échelle des paysages sous-marins. In «Sub-marine seascapes», Agence des Aires Marines Protégées. Ed. Springer.

- **Chapter VI**

CUADROS-CASADO A., CHEMINEE A., et al. (**in prep**). Effect of *Cystoseira barbata* forests restoration on the nursery value of macrophytes-formed rocky habitats for juvenile fish (Menorca Island, SW Mediterranean Sea).

7.2 Main oral presentations

CHEMINEE Adrien, SALA Enric, PASTOR Jérémy, MANGIALAJO Luisa, BODILIS Pascaline, COTTALORDA Jean-Michel, BIANCHIMANI Olivier, ARCEO Hazel and FRANCOUR Patrice ; The FOREFISH Project : objectives and main results – perspectives; International Workshop of the project "Brown algal Biodiversity and Ecology in Eastern Mediterranean Sea". http://www.eastmedit-seaweeds.net/ ; September 2011, Hydrobiological Station of Rhodes Rhodes island, Greece.

CHEMINEE Adrien, SALA Enric, PASTOR Jérémy, MANGIALAJO Luisa, BODILIS Pascaline, COTTALORDA Jean-Michel, BIANCHIMANI Olivier, ARCEO Hazel and FRANCOUR Patrice ; Les forêts à *Cystoseira* (Phaeophycées) et le renouvellement des assemblages de poissons (Téléostéens) des fonds rocheux Méditerranéens ; Colloque de la Société Phycologique de France ; April 2011 ; Villefranche-sur-mer , France.

CHEMINEE Adrien, THIRIET Pierre and FRANCOUR Patrice ; Les forêts de Cystoseires (*Cystoseira* spp.) : Rôle de nurserie, fonctionnement écosystémique et conséquences potentielles de leur rétrogression ; SEMINAIRE SCIENTIFIQUE ET TECHNIQUE « Paysages sous-marins » ; March 2011, Océanopolis, Brest, France

CHEMINEE Adrien, MANGIALAJO Luisa and FRANCOUR Patrice ; Algal forests and the replenishment of Mediterranean rocky fishes; ICES Annual Science Conference; September 2010, Nantes France.

CHEMINEE Adrien, MANGIALAJO Luisa and FRANCOUR Patrice; The FOREFISH Project : Algal forests and the replenishment of Mediterranean rocky fishes; SER Avignon symposium; August 2010, Avignon, France.

CHEMINEE Adrien, FRANCOUR Patrice and HARMELIN-VIVIEN Mireille; Assessment of *Diplodus* spp. (Sparidae) nursery grounds along Marseilles rocky shore (France, NW Mediterranean) ; 4ème Rencontres de l'Ichtyologie en France; March 2009, Paris, France.

7.3 University lectures for students

The data I gathered during my PhD thesis allowed me to illustrate various lectures and practical works I gave to University students, every year from 2008 to 2012:

- Master, Université de Nice : Management of coastal areas (12 h)

- Master of Oceanography, Université Pierre et Marie Curie : ecology and identification of coastal fishes (5 h)
- Master of Oceanography, Université Aix-Marseille : applied marine ecology (field course) - ecology and identification of coastal fishes (8 h)
- Licence (undergraduate studies) of Biology, Université de Nice : ecology of coastal fishes (2 h)
- Licence (undergraduate studies) of Biology, Université de Nice : biodiversity and fragmentation of seascapes (8 h)

7.4 Vulgarization of scientific knowledge

7.4.1 Conferences

Exemple : « Pourquoi et comment observer les nurseries des juvéniles de poissons méditerranéens? Expériences scientifiques originales en Rade de Villefranche-sur-Mer» ; Séminaire de vulgarisation scientifique au Café des Sciences co-organisé par L'Espace Trinquette - L'Association Océanides - les chercheurs du CNRS 06 - Jeudi 17 Novembre 2011, Villefranche-sur-Mer (France).

7.4.2 Web site and video documentary

I coordinated the realization of a web site and underwater documentary focusing on the « FOREFISH project », in the frame of which this PhD thesis have been done. The documentary was realized by J. Espla (Poisson-Lune Productions) during the year 2010, subtitled in English, and participated in the World Festival of Underwater Pictures in October 2011 (http://www.underwater-festival.com/).

Website and documentary are available at http://www.unice.fr/ecomers/ (Fig. 1,2).

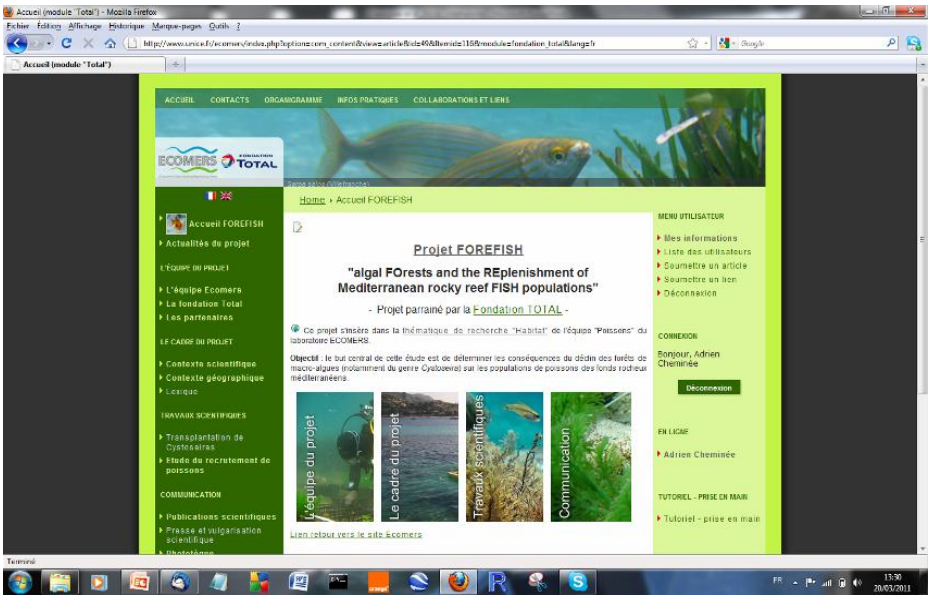


Fig. 1 : FOREFISH Project website

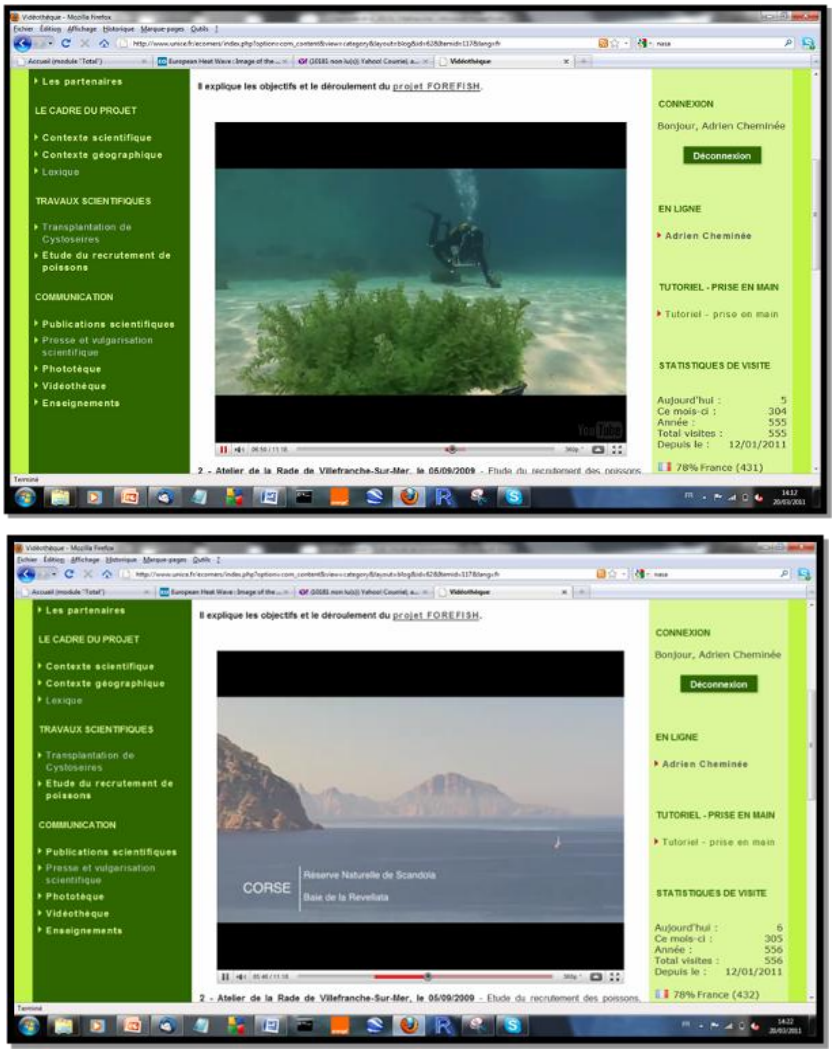


Figure 2 : the online underwater documentary

References

An antic mosaic in a palace from Rhodos Island, Greece, South-eastern Mediterranean (September 2011) – Maybe some Sparidae?

References

Abesamis, R.A., Russ, G.R., Alcala, A.C., 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. Aquatic Conservation: Marine and Freshwater Ecosystems 16(4), 349-371.

Abrams, P.A., 1990. The Evolution of Anti-Predator Traits in Prey in Response to Evolutionary Change in Predators. Oikos 59(2), 147-156.

Aburto-Oropeza, O., Sala, E., Paredes, G., Mendoza, A., Ballesteros, E., 2007. Predictability of reef fish recruitment in a highly variable nursery habitat. Ecology 88(9), 2220-2228.

Anderson, M., Gorley, R., Clarke, K., 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. Primer-e, Plymouth, UK, pp. 214.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58(3), 626-639.

Anderson, M.J., Millar, R.B., 2004. Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. Journal of Experimental Marine Biology and Ecology 305(2), 191-221.

Anholt, B.R., Werner, E.E., 1998. Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. Evol. Ecol. 12(6), 729-738.

Arceo, H., Cheminée, A., Bodilis, P., Mangialajo, P., Francour, P., 2012. Fishery reserve effects on sparid recruitment along French Mediterranean coasts, Proceedings of the 12th International Coral Reef Symposium Cairns, Australia, 9-13 July 2012.

Attrill, M.J., Strong, J.A., Rowden, A.A., 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? Ecography 23(1), 114-121.

August, P.V., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. Ecology 64(6), 1495-1507.

Baker, J., French, K., Whelan, R.J., 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology 83(11), 3048-3059.

Ballesteros, E., 1992. Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució. Arxius de la Secció de Ciències, Institut d'Estudis Catalans 101, Barcelona.

Ballesteros, E., Sala, E., Garrabou, J., Zabala, M., 1998. Community structure and frond size distribution of a deep water stand of *Cystoseira spinosa* (Phaeophyta) in the northwestern Mediterranean. Eur. J. Phycol. 33(2), 121-128.

Ballesteros, E., Garrabou, J., Hereu, B., Zabala, M., Sala, E., 1999. *Cystoseira* 1999, Rapport Mission Scandola. Travaux scientifiques du Parc naturel Régional de Corse.

Ballesteros, E., Hereu, B., Cebrian, E., Weitzmann, B., Navarro, L., 2010. Rapport mission Scandola: *Cystoseira* 2010. Travaux Scientifiques du Parc Naturel Régional de Corse, 32.

Ballesteros, E., Hereu, B., Zabala, M., Alcoverro, T., Garrabou, J., Sala, E., 2002. Rapport mission Scandola: *Cystoseira* 2000. Travaux Scientifiques du Parc Naturel Régional de Corse 60, 95-115.

Bariche, M., Letourneur, Y., Harmelin-Vivien, M., 2004. Temporal Fluctuations and Settlement Patterns of Native and Lessepsian Herbivorous Fishes on the Lebanese Coast (Eastern Mediterranean). Environmental Biology of Fishes 70(1), 81-90.

Basterretxea, G., Jordi, A., CatalÁN, I.A., SabatÉS, A.N.A., 2012a. Model-based assessment of local-scale fish larval connectivity in a network of marine protected areas. Fisheries Oceanography 21(4), 291-306.

Basterretxea, G., Jordi, A., Catalan, I.A., Sabates, A., 2012b. Model-based assessment of local-scale fish larval connectivity in a network of marine protected areas. Fisheries Oceanography, no-no.

Beck, M.W., Heck, K.L., Able, K.W., Childers, D.L., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F., Weinstein, M.P., 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51(8), 633-641.

Bell, J.D., Harmelin-Vivien, M.L., 1983. Fish fauna of French Mediterranean Posidonia oceanica seagrass meadows. II: feeding habits. Multilingue 11(1), 14.

Bell, J.D., Westoby, M., 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68(2), 205-209.

Bell, J.D., Westoby, M., Steffe, A.S., 1987. Fish larvae settling in seagrass - Do they discriminate between beds of different leaf density. Journal of Experimental Marine Biology and Ecology 111(2), 133-144.

Bodilis, P., Arceo, H., Francour, P., 2011. Further evidence of the establishment of *Fistularia commersonii* (Osteichthyes: Fistulariidae) in the north-western Mediterranean Sea. Marine Biodiversity Records 4, 1-4.

Bonaviri, C., Vega Fernández, T., Fanelli, G., Badalamenti, F., Gianguzza, P., 2011. Leading role of the sea urchin *Arbacia lixula* in maintaining the barren state in southwestern Mediterranean. Marine Biology 158(11), 2505-2513.

Box, A., Martin, D., Deudero, S., 2010. Changes in seagrass polychaete assemblages after invasion by *Caulerpa racemosa* var. *cylindracea* (Chlorophyta: Caulerpales): community structure, trophic guilds and taxonomic distinctness. Scientia Marina 74(2), 317-329.

Bussotti, S., Guidetti, P., 2010. Timing and habitat preferences for settlement of juvenile fishes in the Marine Protected Area of Torre Guaceto (south-eastern Italy, Adriatic Sea). Italian Journal of Zoology 78(2), 243-254.

Carr, M.H., 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology 126(1), 59-76.

Carr, M.H., 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75(5), 1320-1333.

Cebrian, E., Linares, C., Marschal, C., Garrabou, J., 2012. Exploring the effects of invasive algae on the persistence of gorgonian populations. Biological Invasions, 1-10.

Chapman, M., 1995. Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. Mar. Ecol.-Prog. Ser. 126, 191-202.

Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Marine Biology 140(5), 981-990.

Cheminée, A., 2002. Appui à l'inscription de sites mahorais sur la liste de Ramsar. Maîtrise, Université Aix-Marseille III, 23.

Cheminée, A., Francour, P., Harmelin-Vivien, M., 2011. Assessment of *Diplodus* spp. (Sparidae) nursery grounds along the rocky shore of Marseilles (France, NW Mediterranean). Scientia Marina 75(1), 181-188.

Cheminée, A., Sala, E., Pastor, J., Bodilis, P., Thiriet, P., Mangialajo, L., Cottalorda, J.-M., Francour, P., under review. Nursery value of *Cystoseira* forests for Mediterranean rocky reef fishes under review at JEMBE.

Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. Marine Ecology-Progress Series 396, 221-233.

Clarisse, S., 1984. Apport de différentes techniques cartographiques à la connaissance de l'autoécologie de *Cystoseira balearica* Sauvageau, macroalgue marine dominante dans la région de Calvi (Corse). Lejeunia 113, 1-24.

Clarke, K.R., Gorley, R.N., 2006. Primer v6: User Manual/Tutorial - Primer-E Ltd. 190 pp.

Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: A regional meta-analysis in the Mediterranean Sea. Biol. Conserv. 143(9), 2195-2206.

Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.A., Goñi, R., Borg, J.A., Forcada, A., de Lucia, G.A., Pérez-Ruzafa, Á., Afonso, P., Brito, A., Guala, I., Diréach, L.L., Sanchez-Jerez, P., Somerfield, P.J., Planes, S., 2010. Marine reserves: Fish life history and ecological traits matter. Ecological Applications 20(3), 830-839.

Coll, J., Linde, M., García-Rubies, A., Riera, F., Grau, A.M., 2004. Spear fishing in the Balearic Islands (west central Mediterranean): species affected and catch evolution during the period 1975–2001. Fisheries Research 70(1), 97-111.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froglia, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C.M., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., San Vicente, C., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E., 2010. The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. PLoS ONE 5(8), e11842.

Connell, S.D., Jones, G.P., 1991. The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. Journal of Experimental Marine Biology and Ecology 151(2), 271-294.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Annual Review of Marine Science 1, 443-466.

Cowen, R.K., Gawarkiewicz, G.G., Pineda, J., Thorrold, S.R., Werner, F.E., 2007. Population connectivity in marine systems : an overview. Oceanography Society.

Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8), 2227-2240.

Daniel, B., Piro, S., Charbonnel, E., Francour, P., Letourneur, Y., 2009. Lessepsian rabbitfish *Siganus luridus* reached the French Mediterranean coasts. Cybium 33(2), 163-164.

David, G., Mirault, É., 2009. Fonctions et logiques d'interface des récifs coralliens sur le littoral de la Réunion. Communication présentée aux XIe Journées de Géographie tropicale,«Les interfaces. Ruptures, transitions et mutations», 7-10 novembre 2005, et actualisée en décembre 2009. Les Cahiers d'Outre-Mer. Revue de géographie de Bordeaux 62(248), 571-588.

David, G., Lo, H., Soule, M., 2003. Le parc marin de Mohéli (Comores): de la protection des tortues à la gestion de l'espace insulaire, Les aires protégées insulaires et littorales tropicales, pp. 121-135.

Dayton, P.K., 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16, 215-245.

Deza, A.A., Anderson, T.W., 2010. Habitat fragmentation, patch size, and the recruitment and abundance of kelp forest fishes. Mar. Ecol.-Prog. Ser. 416, 229-240.

Di Franco, A., Guidetti, P., 2011. Patterns of variability in early-life traits of fishes depend on spatial scale of analysis. Biology Letters 7(3), 454-456.

Di Franco, A., De Benedetto, G., De Rinaldis, G., Raventos, N., Sahyoun, R., Guidetti, P., 2011. Large scale-variability in otolith microstructure and microchemistry: The case study of Diplodus sargus sargus (Pisces: Sparidae) in the Mediterranean Sea. Ital. J. Zoolog. 78(2), 182-192.

Di Franco, A., Gillanders, B.M., De Benedetto, G., Pennetta, A., De Leo, G.A., Guidetti, P., 2012. Dispersal patterns of coastal fish: implications for designing networks of marine protected areas. PLoS ONE.

Direction de l'Agriculture de Mayotte, Carex Environnement, ARVAM, WWF, 2002. Volet 4 du Plan de Gestion du Lagon de Mayotte : Appui au classement RAMSAR de certaines zones humides. In: Carex (Ed.).

DREAL_PACA, 2012. http://carmen.developpement-durable.gouv.fr/25/environnement.map 06/02/2012.

Eckert, G.J., 1985. Settlement of coral reef fishes to different natural substrata and at different depths. In: Harmelin-Vivien, M., Salvat, B. (Eds.), 5th Int Coral Reef Congress Volume 5 : Miscellaneous papers (A). Antenne Museum-EPHE, Moorea, French Polynesia, Tahiti, pp. 385-390.

Figuier, L., 1869. The ocean world. D. Appleton & Co., New York.

Fisher, P., Weber, A., Heine, G., Weber, H., 2007. Habitat structure and fish: assessing the role of habitat complexity for fish using a small, semiportable, 3-D underwater observatory. Limnology and Oceanography: Methods 5, 12.

Francour, P., 1999. A critical review of adult and juvenile fish sampling techniques in *Posidonia oceanica* seagrass beds. Naturalista sicil. 23 (Supp.), 33-57.

Francour, P., Le Direac'h, L., 1994. Recrutement de l'ichtyofaune dans l'herbier superficiel à *Posidonia oceanica* de la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale): données préliminaires. Travaux Scientifiques du Parc Naturel Régional Corse 46, 71–91.

Francour, P., Le Direac'h, L., 2001. Analyse spatiale du recrutement des poissons de l'herbier à *Posidonia oceanica* dans la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale). Contrat Parc Naturel Régional de la Corse & GIS Posidonie. LEML publ. Nice, 1-23.

Francour, P., Ganteaume, A., Poulain, M., 1999. Effects of boat anchoring in Posidonia oceanica seagrass beds in the Port-Cros National Park (north-western Mediterranean Sea). Aquatic Conservation: Marine and Freshwater Ecosystems 9(4), 391-400.

Francour, P., Harmelin-Vivien, M., Harmelin, J.G., Duclerc, J., 1995. Impact of *Caulerpa taxifolia* colonization on the littoral ichthyofauna of North-Western Mediterranean sea: preliminary results. Hydrobiologia 300-301(1), 345-353.

Francour, P., Harmelin, J.-G., Pollard, D., Sartoretto, S., 2001. A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquatic Conservation: Marine and Freshwater Ecosystems 11(3), 155-188.

Francour, P., Pellissier, V., Mangialajo, L., Buisson, E., Stadelmann, B., Veillard, N., Meinesz, A., ThiBaut, T., Vaugelas, J.d., 2009. Changes In invertebrate assemblages of Posidonia oceanica beds following Caulerpa taxifolia Invasion. Vie et Milieu 59(1), 31-38.

Froese, F., Pauly, D., 2011. www.fishbase.org December 10.

Gabrié, C., Eynaudi, A., Cheminée, A., 2007. Les récifs coralliens protégés de l'outre-mer français. . IFRECOR, 104 pp.

Garcia-Rubies, A., Macpherson, E., 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the mediterranean littoral. *Marine Biology* 124(1), 35-42.

Garcia-Rubies, A., Mateo, M.A., Hereu, B., Coma, R., Teixidó, T., Garrabou, Q., Bonaviri, C., Linares, C., Zabala, M., Cebrian, E., Navarro, L., Weitzmann, B., Cheminée, A., Plyuscheva, M., Serrano, E., 2009. Preliminary assessment of the impact of an extreme storm on Catalan Mediterranean shallow benthic communities. Plinius Conference Abstracts, 11th Plinius Conference on Mediterranean Storms Vol. 11(Plinius11-52-1).

Giakoumi, S., Cebrian, E., Kokkoris, G.D., Ballesteros, E., Sala, E., 2011. Relationships between fish, sea urchins and macroalgae: The structure of shallow rocky sublittoral communities in the Cyclades, Eastern Mediterranean. Estuarine, Coastal and Shelf Science(0).

Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology Progress Series 247, 281-295.

GIP_Calanques, 2012. http://www.gipcalanques.fr/racine/accueil 06/02/2012.

Godoy, E.A.S., Coutinho, R., 2002. Can artificial beds of plastic mimics compensate for seasonal absence of natural beds of *Sargassum furcatum*? ICES Journal of Marine Science 59, S111-S115.

Goni, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Renones, O., Criquet, G., Polti, S., Cadiou, G., Valle, C., Lenfant, P., Bonhomme, P., Perez-Ruzafa, A., Sanchez-Lizaso, J.L., Garcia-Charton, J.A., Bernard, G., Stelzenmuller, V., Planes, S., 2008. Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. Mar. Ecol.-Prog. Ser. 366, 159-174.

Google_Inc., 2011. http://www.google.fr/intl/fr/earth/index.html.

Granek, E.F., Brown, M.A., 2005. Co-Management Approach to Marine Conservation in Mohéli, Comoros Islands - Estrategia de Cogestión para la Conservación Marina en Mohéli, Islas Comoros. Conservation Biology 19(6), 1724-1732.

Grober-Dunsmore, R., Pittman, S.J., Caldow, C., Kendall, M.S., Frazer, T.K., 2009. A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. Ecological Connectivity among Tropical Coastal Ecosystems, 493-530.

Grüss, A., Kaplan, D.M., Guénette, S., Roberts, C.M., Botsford, L.W., 2011. Consequences of adult and juvenile movement for marine protected areas. Biol. Conserv. 144(2), 692-702.

Guidetti, P., 2000. Differences Among Fish Assemblages Associated with Nearshore Posidonia oceanica Seagrass Beds, Rocky–algal Reefs and Unvegetated Sand Habitats in the Adriatic Sea. Estuarine, Coastal and Shelf Science 50(4), 515-529.

Guidetti, P., 2004. Consumers of sea urchins, *Paracentrotus lividus* and *Arbacia lixula*, in shallow Mediterranean rocky reefs. Helgoland Marine Research 58(2), 110-116.

Guidetti, P., Bussotti, S., 1997. Recruitment of *Diplodus annularis* and *Spondyliosoma cantharus* (Sparidae) in shallow seagrass beds along the Italian coasts (Mediterranean Sea). Marine Life 7, 47-52.

Guidetti, P., Bussotti, S., 2000. Fish fauna of a mixed meadow composed by the seagrasses Cymodocea nodosa and Zostera noltii in the Western Mediterranean. Oceanologica Acta 23(7), 759-770.

Guidetti, P., Fabiano, M., 2000. The Use of Lepidochronology to Assess the Impact of Terrigenous Discharges on the Primary Leaf Production of the Mediterranean Seagrass Posidonia oceanica. Mar. Pollut. Bull. 40(5), 449-453.

Guidetti, P., Vierucci, E., Bussotti, S., 2008. Differences in escape response of fish in protected and fished Mediterranean rocky reefs. Journal of the Marine Biological Association of the United Kingdom 88(03), 625-627.

Guidetti, P., Fraschetti, S., Terlizzi, A., Boero, F., 2003. Distribution patterns of sea urchins and barrens in shallow Mediterranean rocky reefs impacted by the illegal fishery of the rock-boring mollusc *Lithophaga lithophaga*. Marine Biology 143(6), 1135-1142.

Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin, 173-182.

Hansen, J.P., Sagerman, J., Wikstrom, S.A., 2010. Effects of plant morphology on small-scale distribution of invertebrates. Marine Biology 157(10), 2143-2155.

Harborne, A., Mumby, P., Ferrari, R., 2011a. The effectiveness of different meso-scale rugosity metrics for predicting intra-habitat variation in coral-reef fish assemblages. Environmental Biology of Fishes, 1-12.

Harborne, A.R., Mumby, P.J., Kennedy, E.V., Ferrari, R., 2011b. Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. Marine Ecology Progress Series 437(15), 201-214.

Harmelin-Vivien, M., Francour, P., Harmelin, J., Le Direac'h, L., 2001. Dynamics of fish assemblage alterations caused by the introduced alga *Caulerpa taxifolia* near Menton (France). In: Gravez V., R.S., Boudouresque C.F. Le Direach L., Meinesz A., Scabbia G. & Verlaque M. (Ed.), 4 International Workshop on *Caulerpa taxifolia*. GIS Posidonie, pp. 236-245.

Harmelin-Vivien, M.L., Harmelin, J.G., Leboulleux, V., 1995. Microhabitat requirements for settlement of juvenile Sparid fishes on Mediterranean rocky shores. *Hydrobiologia* 301, 309-320.

Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P., Barnabé, G., Blanc, F., Chevalier, R., Duclerc, J., Lasserre, G., 1985. Évaluation visuelle des peuplements et populations de Poissons : méthodes et problèmes. Rev. Ecol. (Terre vie) 40, 467-539.

Harmelin, J.G., Vigliola, L., 1998. Renouvellement des populations de sars (*Diplodus* spp.) du parc national de Port-Cros : évaluation du potentiel. . Rap. Tech. Parc National Port-Cros, Programme Rech. 1996-97, 96.028.83400 PC.

Heck, K., Orth, R., 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Estuarine Perspectives. Kennedy, Academic Press Inc., 449-464.

Heck, K., Hays, G., Orth, R., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253, 123-136.

Hereu, B., 2004. The role of trophic interactions between fishes, sea urchins and algae in the northwest Mediterranean rocky infralittoral. PhD thesis, Universitat de Barcelona, i-xii + 1-237.

Hindell, J.S., Jenkins, G.P., Keough, M.J., 2000. Evaluating the impact of predation by fish on the assemblage structure of fishes associated with seagrass (Heterozostera tasmanica) (Martens ex Ascherson) den Hartog, and unvegetated sand habitats. Journal of Experimental Marine Biology and Ecology 255(2), 153-174.

Hoffmann, L., Renard, R., Demoulin, V., 1992. Phenology, growth and biomass of *Cystoseira balearica* in Calvi (Corsica). Mar. Ecol.-Prog. Ser. 80, 249-254.

Hoffmann, L., Clarisse, S., Detienne, X., Goffart, A., Renard, R., Demoulin, V., 1988. Evolution of the populations of *Cystoseira balearica* (Phaeophyceae) and epiphytic Bangiophyceae in the Bay of Calvi (Corsica) in the last eight years. Bulletin de la Société Royale de Liège 4-5, 263-273.

Horinouchi, M., Sano, M., 1999. Effects of changes in seagrass shoot density and leaf height on abundances and distribution patterns of juveniles of three gobiid fishes in a *Zostera marina* bed. Marine Ecology Progress Series 183, 87-94.

Horinouchi, M., Mizuno, N., Jo, Y., Fujita, M., Sano, M., Suzuki, Y., 2009a. Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. Marine Ecology-Progress Series 377, 43-49.

Horinouchi, M., Mizuno, N., Jo, Y., Fujita, M., Sano, M., Suzuk, i.Y., 2009b. Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. Mar. Ecol.-Prog. Ser. 377, 43-49.

INEA, CNRS, EPHE, IRD, Gil-Cros, S., 2009. Application du concept de solidarité écologique dans les Parcs nationaux - Tome 2 : Approche opérationnelle - rencontre des Parcs nationaux. In: INEA-pub. (Ed.).

Irisson, J.O., 2008. Approche comportementale de la dispersion larvaire en milieu marin. PhD Thesis, University of Perpignan, EPHE, Perpignan.

Irisson, J.O., Guigand, C., Paris, C.B., 2009. Detection and quantification of marine larvae orientation in the pelagic environment. Limnol. Oceanogr. Methods 7, 664-672.

Jelbart, J.E., Ross, P.M., Connolly, R.M., 2006. Edge effects and patch size in seagrass landscapes: an experimental test using fish. Mar. Ecol.-Prog. Ser. 319, 93-102.

Jones, G., Almany, G., Russ, G., Sale, P., Steneck, R., van Oppen, M., Willis, B., 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28(2), 307-325.

Jones, G.P., 1984. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch & Schneider (Pisces: Labridae). I. Factors influencing recruitment. Journal of Experimental Marine Biology and Ecology 75(3), 257-276.

Juanes, F., 2007. Role of habitat in mediating mortality during the post-settlement transition phase of temperate marine fishes. Journal of Fish Biology 70(3), 661-677.

Kenyon, R.A., Haywood, M.D.E., Heales, D.S., Loneragan, N.R., Pendrey, R.C., Vance, D.J., 1999. Abundance of fish and crustacean postlarvae on portable artificial seagrass units: daily sampling provides quantitative estimates of the settlement of new recruits. Journal of Experimental Marine Biology and Ecology 232(2), 197-216.

Klein, J., Verlaque, M., 2008. The *Caulerpa racemosa* invasion: A critical review. Mar. Pollut. Bull. 56(2), 205-225.

Knowlton, N., 2004. Multiple “stable” states and the conservation of marine ecosystems. Progress In Oceanography 60(2-4), 387-396.

Koenig, C.C., Coleman, F.C., Grimes, C.B., Fitzhugh, G.R., Scanlon, K.M., Gledhill, C.T., Grace, M., 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. Bulletin of Marine Science 66(3), 593-616.

La Mesa, G., Louisy, P., Vacchi, M., 2002. Assessment of microhabitat preferences in juvenile dusky grouper (*Epinephelus marginatus*) by visual sampling. Marine Biology 140(1), 175-185.

Le Direac'h, L., Francour, P., 1998. Recrutement de *Diplodus annularis* (Sparidae) dans les herbiers de posidonie de la Réserve Naturelle de Scandola (Corse). Travaux Scientifiques du Parc Naturel Régional Corse 57, 42-75.

Lejeune, P., 1984. Etude ecoethologique des comportements reproducteurs et sociaux des Labridae mediterraneens des genres *Symphodus* RAFINESQUE, 1810 et *Coris* LACEPEDE, 1802. PhD thesis, Université de Liège, 231 pp.

Lejeune, P., 1985. Le comportement social des Labridés méditerranéens. Cahier d'Ethologie Appliquée 5(2), 208.

Letourneur, Y., Ruitton, S., Sartoretto, S., 2003. Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. Journal of the Marine Biological Association of the United Kingdom 83(01), 193-204.

Levi, F., 2004. Etude de l'impact de l'algue envahissante *Caulerpa taxifolia* sur les peuplements de poissons - Etude approfondie sur une espèce « modèle » : *Symphodus ocellatus* (Labridae). PhD thesis, Université de Nice Sophia-Antipolis 269.

Levi, F., Francour, P., 2004. Behavioural response of *Mullus surmuletus* to habitat modification by the invasive macroalga *Caulerpa taxifolia*. Journal of Fish Biology 64(1), 55-64.

Levin, P., Petrik, R., Malone, J., 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. Oecologia 112(1), 55-63.

Levin, P.S., 1994. Fine-scale temporal variation in recruitment of a temperate demersal fish: the importance of settlement versus post-settlement loss. Oecologia 97(1), 124-133.

Levin, P.S., Hay, M.E., 1996. Responses of temperate reef fishes to alterations in algal structure and species composition. Mar. Ecol.-Prog. Ser. 134(1-3), 37-47.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15, 237–240.

Lima, S.L., 1992. STRONG PREFERENCES FOR APPARENTLY DANGEROUS HABITATS - A CONSEQUENCE OF DIFFERENTIAL ESCAPE FROM PREDATORS. Oikos 64(3), 597-600.

Lima, S.L., 1998. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. Stress and Behavior 27, 215-290.

Lima, S.L., Dill, L.M., 1990. BEHAVIORAL DECISIONS MADE UNDER THE RISK OF PREDATION - A REVIEW AND PROSPECTUS. Can. J. Zool.-Rev. Can. Zool. 68(4), 619-640.

Longepierre, S., Robert, A., Levi, F., Francour, P., 2005. How an invasive alga species (*Caulerpa taxifolia*) induces changes in foraging strategies of the benthivorous fish *Mullus surmuletus* in coastal Mediterranean ecosystems. Biodiversity and Conservation 14(2), 365-376.

Louisy, P., 2002. Guide d'identification des poissons marins - Europe de l'ouest et Méditerranée. Ulmer, 430 pp.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton Univ Pr.

MacPherson, E., 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. Journal of Experimental Marine Biology and Ecology 220(1), 127-150.

Macpherson, E., Zika, U., 1999. Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean. Mar. Ecol.-Prog. Ser. 182, 269-282.

Macpherson, E., Raventos, N., 2005. Settlement patterns and post-settlement survival in two Mediterranean littoral fishes: influences of early-life traits and environmental variables. Marine Biology 148(1), 167-177.

Macpherson, E., Biagi, F., Francour, P., García-Rubies, A., Harmelin, J., Harmelin-Vivien, M., Jouvenel, J.Y., Planes, S., Vigliola, L., Tunesi, L., 1997. Mortality of juvenile fishes of the genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. Marine Ecology Progress Series 160, 135-147.

Macreadie, P.I., Hindell, J.S., Keough, M.J., Jenkins, G.P., Connolly, R.M., 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91(7), 2013-2021.

Mangialajo, L., Chiantore, M., Cattaneo-Vietti, R., 2008. Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. Mar. Ecol.-Prog. Ser. 358, 63.

Mangialajo, L., Ruggieri, N., Asnaghi, V., Chiantore, M., Povero, P., Cattaneo-Vietti, R., 2007. Ecological status in the Ligurian Sea: The effect of coastline urbanisation and the importance of proper reference sites. Mar. Pollut. Bull. 55(1-6), 30-41.

Martin, C.W., Fodrie, F.J., Heck, K.L., Mattila, J., 2010. Differential habitat use and antipredator response of juvenile roach (Rutilus rutilus) to olfactory and visual cues from multiple predators. Oecologia 162(4), 893-902.

Matsuda, H., Abrams, P.A., Hori, H., 1993. THE EFFECT OF ADAPTIVE ANTIPREDATOR BEHAVIOR ON EXPLOITATIVE COMPETITION AND MUTUALISM BETWEEN PREDATORS. Oikos 68(3), 549-559.

McCook, L., Almany, G., Berumen, M., Day, J., Green, A., Jones, G., Leis, J., Planes, S., Russ, G., Sale, P., Thorrold, S., 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28(2), 353-366.

MEDDTL, MAAPRAT, IGN, BRGM, 2012. http://www.geoportail.fr/index.do 06/02/2012.

Meinesz, A., Hesse, B., 1991. Introduction of the tropical alga *Caulerpa taxifolia* and its invasion of the Northwestern Mediterranean. Oceanologica acta 14(4), 415-426.

Meinesz, A., Cottalorda, J.M., Chiaverini, D., Cassar, N., De Vaugelas, J., 1998. Suivi de l'invasion de l'algue *Caulerpa taxifolia* en Méditerranée : situation au 31 décembre 1997. Laboratoire Environnement Marin Littoral de l'Université de Nice-Sophia Antipolis publ., 237 p.

Meinesz, A., Javel, F., Longepierre, S., Vaugelas, J.d., Garcia, D., 2006. www.medam.org 06/02/2012.

Milazzo, M., Badalamenti, F., Riggio, S., Chemello, R., 2004a. Patterns of algal recovery and small-scale effects of canopy removal as a result of human trampling on a Mediterranean rocky shallow community. Biol. Conserv. 117(2), 191-202.

Milazzo, M., Badalamenti, F., Ceccherelli, G., Chemello, R., 2004b. Boat anchoring on *Posidonia oceanica* beds in a marine protected area (Italy, western Mediterranean): effect of anchor types in different anchoring stages. Journal of Experimental Marine Biology and Ecology 299(1), 51-62.

Molenaar, H., Meinesz, A., Thibaut, T., 2009. Alterations of the structure of *Posidonia oceanica* beds due to the introduced alga *Caulerpa taxifolia*. Scientia Marina 73(2), 329-335.

Montefalcone, M., Parravicini, V., Vacchi, M., Albertelli, G., Ferrari, M., Morri, C., Bianchi, C.N., 2010. Human influence on seagrass habitat fragmentation in NW Mediterranean Sea. Estuarine, Coastal and Shelf Science 86(2), 292-298.

Morat, F., Mante, A., Drunat, E., Dabat, J., Bonhomme, P., Harmelin-Vivien, M., Letourneur, Y., 2011. Diet of the Mediterranean European shag, Phalacrocorax aristotelis desmarestii, its ecological significance and interaction with local fisheries in the Riou Archipelago (Marseilles, France). Vie et Milieu 61(2), 77-86.

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136(1), 1-13.

Morris, D.W., 2011. Adaptation and habitat selection in the eco-evolutionary process. Proc. R. Soc. B-Biol. Sci. 278(1717), 2401-2411.

Mouillot, D., Albouy, C., Guilhaumon, F., Ben Rais Lasram, F., Coll, M., Devictor, V., Meynard, Christine N., Pauly, D., Tomasini, Jean A., Troussellier, M., Velez, L., Watson, R., Douzery, Emmanuel J.P., Mouquet, N., 2011. Protected and Threatened Components of Fish Biodiversity in the Mediterranean Sea. Current Biology 21(12), 1044-1050.

Mumby, P.J., 2006. Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. Biol. Conserv. 128(2), 215-222.

Nanjo, K., Nakamura, Y., Horinouchi, M., Kohno, H., Sano, M., 2011. Predation risks for juvenile fishes in a mangrove estuary: A comparison of vegetated and unvegetated microhabitats by tethering experiments. Journal of Experimental Marine Biology and Ecology 405(1-2), 53-58.

Navarro, L., Ballesteros, E., Linares, C., Hereu, B., 2011. Spatial and temporal variability of deep-water algal assemblages in the Northwestern Mediterranean: The effects of an exceptional storm. Estuarine, Coastal and Shelf Science 95(1), 52-58.

O'Brien, W.J., 1979. The Predator-Prey Interaction of Planktivorous Fish and Zooplankton: Recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. American Scientist 67(5), 572-581.

Oberlinkels, M., Cheminée, A., Guillaume, P., Deschellette, Y., 2007. Etude de l'état initial de l'environnement - Projet hôtelier à l'Anse Takamaka (Ile de Praslin, Seychelles). GEI, pp. 60.

Olabarria, C., Underwood, A.J., Chapman, M.G., 2002a. Appropriate experimental design to evaluate preferences for microhabitat: an example of preferences by species of microgastropods. Oecologia 132(2), 159-166.

Olabarria, C.O., Underwood, A.U., Chapman, M.C., 2002b. Appropriate experimental design to evaluate preferences for microhabitat: an example of preferences by species of microgastropods. Oecologia 132(2), 159-166.

Ordines, F., Quetglas, A., Massuti, E., Moranta, J., 2009. Habitat preferences and life history of the red scorpion fish, Scorpaena notata, in the Mediterranean. Estuar. Coast. Shelf Sci. 85(4), 537-546.

Ornellas, A.B., Coutinho, R., 1998. Spatial and temporal patterns of distribution and abundance of a tropical fish assemblage in a seasonal *Sargassum* bed, Cabo Frio Island, Brazil. Journal of Fish Biology 53, 198-208.

Parker, J.D., Duffy, J.E., Orth, R.J., 2001. Plant species diversity and composition: experimental effects on marine epifaunal assemblages. Marine Ecology-Progress Series 224, 55-67.

Pergent-Martini, C., Rico-Raimondino, V., Pergent, G., 1994. Primary production of Posidonia oceanica in the Mediterranean Basin. Marine Biology 120(1), 9-15.

Piko, A.A., Szedlmayer, S.T., 2007. Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper. Journal of fish Biology 70(3), 758-769.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environmental Conservation 27(02), 179-200.

Pittman, S., Kneib, R., Simenstad, C., 2011. Practicing coastal seascape ecology. Marine Ecology Progress Series 427, 187-190.

Planes, S., Macpherson, E., Biagi, F., Garcia-Rubies, A., Harmelin, J., Harmelin-Vivien, M., Jouvenel, J.Y., Tunesi, L., Vigliola, L., Galzin, R., 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. Journal of the Marine Biological Association of the United Kingdom 79(1), 137-143.

Polunin, N., Roberts, C., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Mar. Ecol.-Prog. Ser. 100, 167-167.

R_Development_Core_Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing. ISBN: 3-900051-07-0, http://www.R-project.org/

Raventos, N., Macpherson, E., 2001. Planktonic larval duration and settlement marks on the otoliths of Mediterranean littoral fishes. Marine Biology 138(6), 1115-1120.

Raventos, N., Macpherson, E., 2005a. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Mar. Ecol.-Prog. Ser. 285, 205-211.

Raventos, N., Macpherson, E., 2005b. Environmental influences on temporal patterns of settlement in two littoral labrid fishes in the Mediterranean Sea. Estuar. Coast. Shelf Sci. 63(4), 479-487.

Riccato, F., Fiorin, R., Curiel, D., Rismondo, A., Cerasuolo, C., Torricelli, P., 2009. Interazione tra il popolamento ittico e le alghe brune del genere *Cystoseira* in un ambiente di scogliera artificiale del golfo di Venezia. Boll. Mus. civ. St. nat. Venezia 59, 95-108.

Rilov, G., Schiel, D.R., 2011. Community Regulation: The Relative Importance of Recruitment and Predation Intensity of an Intertidal Community Dominant in a Seascape Context. PLoS One 6(8).

Roberts, C.M., 1997. Connectivity and Management of Caribbean Coral Reefs. Science 278(5342), 1454-1457.

Roberts, C.M., Polunin, N.V.C., 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1(1), 65-91.

Rovere, A., Bellati, S., Parravicini, V., Firpo, M., Morri, C., Bianchi, C., 2009. Abiotic and Biotic Links Work Two Ways: Effects on the Deposit at the Cliff Foot Induced by Mechanical Action of Date Mussel Harvesting (*Lithophaga lithophaga*). Estuaries and Coasts 32(2), 333-339.

Sala, E., Boudouresque, C.F., Harmelin-Vivien, M., 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82(3), 425-439.

Sala, E., Kizilkaya, Z., Yildirim, D., Ballesteros, E., 2011. Alien marine fishes deplete algal biomass in the Eastern Mediterranean. PLoS ONE 6(2), e17356.

Sala, E., Ballesteros, E., Dendrinos, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti, S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu, B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S., Micheli, F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr, R., Tomas, F., Zabala, M., 2012. The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications. PLoS ONE 7(2), e32742.

Sale, P.F., 2004. Connectivity, Recruitment Variation, and the Structure of Reef Fish Communities. Integrative and Comparative Biology 44(5), 390-399.

Sales, M., Ballesteros, E., 2009. Shallow Cystoseira (Fucales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): Relationships with environmental factors and anthropogenic pressures. Estuarine, Coastal and Shelf Science 84(4), 476-482.

Sales, M., Ballesteros, E., 2010. Long-term comparison of algal assemblages dominated by *Cystoseira crinita* (Fucales, Heterokontophyta) from Cap Corse (Corsica, North Western Mediterranean). Eur. J. Phycol. 45(4), 404-412.

Sales, M., Ballesteros, E., 2012. Seasonal dynamics and annual production of *Cystoseira crinita* (Fucales: Ochrophyta)-dominated assemblages from the northwestern Mediterranean. Scientia Marina 76(2), 10.

Sales, M., Cebrian, E., Tomas, F., Ballesteros, E., 2011. Pollution impacts and recovery potential in three species of the genus Cystoseira (Fucales, Heterokontophyta). Estuarine, Coastal and Shelf Science.

Sales, M., Ballesteros, E., Anderson, M.J., Iveša, L., Cardona, E., 2012. Biogeographical patterns of algal communities in the Mediterranean Sea: Cystoseira crinita-dominated assemblages as a case study. Journal of Biogeography 39(1), 140-152.

Savino, J., Stein, R., 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environmental Biology of Fishes 24(4), 287-293.

Schultz, S., Kruschel, C., 2010. Frequency and success of ambush and chase predation in fish assemblages associated with seagrass and bare sediment in an Adriatic lagoon. Hydrobiologia 649(1), 25-37.

Schultz, S., Kruschel, C., Bakran-Petricioli, T., 2009. Influence of seagrass meadows on predator–prey habitat segregation in an Adriatic lagoon. Marine Ecology Progress Series 374, 85-99.

Seytre, C., Francour, P., 2008. Is the Cape Roux marine protected area (Saint-Raphaël, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. Aquatic Living Resources 21(3), 297.

Seytre, C., Francour, P., 2009. The Cap Roux MPA (Saint-Raphaël, French Mediterranean): changes in fish assemblages within four years of protection. ICES Journal of Marine Science: Journal du Conseil 66(1), 180-187.

Shulman, M.J., 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66(3), 1056-1066.

Smith, T.M., Hindell, J.S., Jenkins, G.P., Connolly, R.M., Keough, M.J., 2011. Edge effects in patchy seagrass landscapes: The role of predation in determining fish distribution. Journal of Experimental Marine Biology and Ecology 399(1), 8-16.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60(3), 1129-1157.

Soltan, D., Verlaque, M., François Boudouresque, C., Francour, P., 2001. Changes in Macroalgal Communities in the Vicinity of a Mediterranean Sewage Outfall After the Setting Up of a Treatment Plant. Mar. Pollut. Bull. 42(1), 59-70.

Stergiou, K.I., Karpouzi, V.S., 2001. Feeding habits and trophic levels of Mediterranean fish. Reviews in Fish Biology and Fisheries 11(3), 217-254.

Stoner, A.W., 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, Lagodon rhomboides (Linnaeus). Journal of Experimental Marine Biology and Ecology 58(2-3), 271-284.

Susini, M., Mangialajo, L., Thibaut, T., Meinesz, A., 2007. Development of a transplantation technique of Cystoseira amentacea var. stricta and Cystoseira compressa. Biodiversity in Enclosed Seas and Artificial Marine Habitats, 241-244.

Terlizzi, A., Anderson, M.J., Fraschetti, S., Benedetti-Cecchi, L., 2007. Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. Mar. Ecol.-Prog. Ser. 332, 25-39.

Terradas, J., Prat, N., Escarré, A., Margalef, R., 1989. Historia natural dels paisos Catalans.

Thibaut, T., Pinedo, S., Torras, X., Ballesteros, E., 2005. Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Alberes coast (France, North-western Mediterranean). Mar. Pollut. Bull. 50(12), 1472-1489.

Thiriet, P., Cheminée, A., Francour, P., accepted. Nursery role of macrophytes-formed habitats: abundance patterns and underlying processes under a seascape approach. Proceedings of 'Séminaire scientifique et technique «Paysages sous-marins», Agence des Aires Marines Protégées, Océanopolis, Brest, 29-31 mars 2011'.

Thistle, M.E., Schneider, D.C., Gregory, R.S., Wells, N.J., 2010. Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity. Marine Ecology Progress Series 405, 39-56.

Thompson, J., Cheylan, M., Delanoë, O., 2009. Des fondements scientifiques pour le concept de solidarité écologique. In: INEA (Ed.). INEA, CNRS, EPHE, IRD, Selarl Gis-ros.

Troll, C., 1939. Luftbildplan and okologische bodenforschung. Zeitschraft der Gesellschaft fur Erdkunde Zu Berlin 241-298.

Tupper, M., Juanes, F., 1999. Effects of a Marine Reserve on Recruitment of Grunts (Pisces: Haemulidae) at Barbados, West Indies. Environmental Biology of Fishes 55(1), 53-63.

Turgeon, K., Robillard, A., Grégoire, J., Duclos, V., Kramer, D.L., 2010. Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. Ecology 91(11), 3332-3342.

Underwood, A., 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology: An Annual Review 19.

Underwood, A.J., 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

van de Wolfshaar, K.E., HilleRisLambers, R., Gardmark, A., 2011. Effect of habitat productivity and exploitation on populations with complex life cycles. Marine Ecology-Progress Series 438, 175-184.

Verlaque, M., 1987. Contribution à l'étude du phytobenthos d'un écosystème photophile thermophile marin en Méditerranée Occidentale. Unicersité d'aix-Marseille II. Faculté des Sciences de Luminy, 387.

Verlaque, M., 1994. Checklist of Introduced Plants in the Mediterranean - Origins and Impact on the Environment and Human Activities. Oceanologica Acta 17(1), 1-23.

Vigliola, L., 1998. Contrôle et régulation du recrutement des Sparidés (Poissons, Téléostéens) en Méditerranée : importance des processus pré- et post-installation benthique. Thèse Doct. Sci., Univ. Aix-Marseille II, Marseille, 268pp.

Vigliola, L., Harmelin-Vivien, M., 2001. Post-settlement ontogeny in three Mediterranean reef fish species of the Genus Diplodus. Bulletin of Marine Science 68(2), 271-286.

Vigliola, L., Harmelin-Vivien, M.L., Biagi, F., Galzin, R., Garcia-Rubies, A., Harmelin, J.G., Jouvenel, J.Y., Le Direach-Boursier, L., Macpherson, E., Tunesi, L., 1998. Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean. Mar. Ecol.-Prog. Ser. 168, 45-56.

Worthington, D.G., Westoby, M., Bell, J.D., 1991. Fish larvae settling in seagrass: Effects of leaf density and an epiphytic alga. Australian Journal of Ecology 16 (3), 289-293.

Abstract

The aim of this PhD was to better understand the characteristics and consequences of the transformations of Mediterranean infralittoral fish (Teleostei) nursery habitats, in order to gather useful knowledge for management of coastal areas in Mediterranean regions. Among the seascape mosaic, *Cystoseira* forests, a threatened macrophytes-formed habitat, displayed higher densities of fish juveniles (notably Labridae and Serranidae) than alternate states of rocky bottoms photophilic biocenosis, namely Dictyotales and Sphacelariales bushland and barren grounds. The relatively higher nursery value of *Cystoseira* forests (for *Symphodus* spp.) and of the shallow heterogeneous blocks and pebbles gentle slopes (for *Diplodus* spp.) where consistent through space at both local (1 km) and regional (20 km) scales, although juvenile densities varied significantly in space between sites for a given nursery habitat. The spatial variability of juvenile densities, both across various habitats and among *Cystoseira* forests was notably related to habitat tri-dimensional structure (heterogeneity and complexity); this structure provided refuges for juveniles and influenced namely predation success of their predators. This experimental and observational study demonstrated that habitat human-induced transformations, such as forest fragmentation and cover density decrease critically reduced their nursery value for coastal fishes. Our results suggest that the fish productivity virtually lost in areas where forests have already disappeared may be considerable. Finally, these essential habitats were scarce and not homogenously distributed along the coast: in the case of *Diplodus* spp., less than 10% of the studied rocky shores displayed nursery habitats. Furthermore, the present work highlighted that the current design of management measures did not take into account the spatial distribution of these nursery habitats and the connectivity between all essential habitats at each life stages. A conceptual scheme aiming at adopting such "seascape approach" is proposed, in order to better target conservation efforts and guarantee coastal fish assemblages' replenishment.

Keywords: Mediterranean rocky Infralittoral, seascape mosaic, macrophyte-formed habitats, *Cystoseira* forests, fish juveniles, nursery value, *Symphodus*, *Diplodus*, essential habitats' distribution, coastal management design

Résumé

Cette thèse avait pour objet les habitats de l'Infralittoral rocheux Méditerranéen qui ont un rôle de nourricerie pour les juvéniles de poissons (Téléostéens). Cette étude visait à mieux comprendre leurs caractéristiques et les conséquences de leurs transformations, notamment d'origine anthropique, dans le but de rassembler des données utiles à la gestion des zones côtières. Au sein de la mosaïque paysagère sous-marine, parmi les faciès de la biocénose des macrophytes photophiles de la roche infralittorale, les forêts de Cystoseires forment un habitat à macrophytes arborescentes qui est menacé. Cette thèse a démontré que ces forêts abritaient des densités plus élevées de juvéniles de poissons (notamment Labridae et Serranidae) que celles observées au sein de faciès alternatifs, en particulier les brousses à Dictyotales et Sphacelariales et les faciès de surpâturage. La haute valeur relative de nourricerie, que ce soit des forêts de Cystoseires (pour trois espèces du genre *Symphodus*), ou des petits fonds à blocs et galets (pour les espèces du genre *Diplodus*), a été observée de manière récurrente dans les différents sites littoraux étudiés aussi bien à l'échelle locale (1 km) que régionale (20 à 100 km). Cependant, pour un habitat donné, les densités de juvéniles ont montré une forte variabilité spatiale entre sites. La variabilité spatiale des densités de juvéniles, aussi bien entres sites des forêts à Cystoseires que d'un habitat à l'autre, était notamment associée aux différences de structure tridimensionnelle de l'habitat (hétérogénéité et complexité). Cette structuration fournissait un refuge pour les juvéniles et a en particulier influencé l'efficacité de leurs prédateurs. Ces travaux, sur la base de manipulations expérimentales et d'observations *in situ*, ont démontré que les transformations des habitats, telles que la fragmentation des forêts ou la diminution de la densité de leur couverture, réduisaient drastiquement leurs valeurs de nourricerie pour les poissons côtiers. Ces résultats suggèrent que la productivité en poissons virtuellement perdue, dans les zones où les forêts ont déjà totalement disparu, est considérable. Par ailleurs, ces habitats essentiels se sont avérés rares et in-équitablement distribués le long des côtes : dans le cas des *Diplodus* spp., moins de 10% des côtes rocheuses étudiées présentaient des habitats nourriceries. Enfin, ce travail a mis en évidence que la planification actuelle des mesures de gestion des zones côtières méditerranéennes ne prenait généralement pas en compte la distribution spatiale des habitats nourriceries, ni leur connectivité avec les autres habitats essentiels à chaque étape clef du cycle de vie des poissons. Un schéma conceptuel, visant à adopter une telle « approche paysage » de la gestion, est proposé : il vise à promouvoir une focalisation optimale des efforts de conservation et à garantir ainsi le renouvellement des peuplements de poissons côtiers.

Mots clefs : Infralittoral rocheux Méditerranéen, paysages sous-marins, macrophytes arborescentes, forêts de Cystoseires, juvéniles de poissons, valeur de nourricerie, *Symphodus*, *Diplodus*, distribution des habitats essentiels, plans de gestion des zones côtières